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# RAPPORTS
## ET
# PROCÈS-VERBAUX DES RÉUNIONS

**Volume 140**

**Part I**

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CONTRIBUTIONS
TO
SPECIAL SCIENTIFIC MEETINGS
1954

*Problems and Methods of Sampling Fish Populations.*

*En Commission chez*
ANDR. FRED. HØST & FILS
COPENHAGUE

Prix: Kr. 25.00

Mars 1956

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CHARLOTTENLUND SLOT – DANEMARK

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**Part I**

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# Introduction.

As the convener of "The Special Scientific Meeting on Sampling", held at the meeting of the International Council for the Exploration of the Sea in Paris 1954, I want to express my most sincere thanks to all the contributors to this report, for the many valuable demonstrations and for the broad and yet detailed approach to one of the most important problems in fisheries science.

I would also like to extend special thanks to Mr. R. J. H. Beverton and to Mr. B. B. Parrish who have carried the burdens in collecting and summarizing the papers. Mr. Parrish also served as the reporter of the meeting and has arranged the papers as they appear here.

As I did when introducing the papers at the meeting, I will also here present some of the main problems we have met with when trying to obtain representative samples of our population of skrei.

The ancient fishery for spawning cod—skrei—which takes place in Lofoten in northern Norway has been subject to statistical analyses and scientific investigations for nearly a hundred years. There is no other fishery in Norway which has been carried on with less changes in fishing methods.

In spite of considerable fluctuations in the annual catches the Lofoten fishery must be called a stable fishery.

Considerable knowledge of the stock has been gained through the long series of observations on the age and size composition of the cod. However, with increased knowledge it was obvious that the sampling was biased by gear selectivity and by segregation in place and time of the spawning fish.

Thus when comparing the average size of fish taken on longlines and handlines with that of fish caught in gill nets, it was found that the net cod was considerably larger. Also the sex ratio was different. In nets we found 60% males and 40% females, on longlines and handlines 60% females and 40% males. It is also worth while mentioning that codliver oil plants prefer the net-caught cod because their livers contain more fat.

The coastline of the Lofoten Islands facing the Vestfjord and the spawning banks is about 100 miles long.

There is a clear tendency of the larger fish to continue into the innermost part of the fjord and of the smaller fish to stop in the outer parts. But within this main pattern we find considerable differences in the size composition on the various spawning banks. It is an inexplicable fact that these differences seem to be rather constant from year to year.

Examining the samples throughout the whole season from January to April we can follow a consistent change in age composition and sex ratio.

In the early samples the older females are in abundance, then gradually the older males increase in number. Simultaneously the younger females become more numerous, and in the latest samples the younger males follow up.

The sampling problem met with in Lofoten is therefore of a combined nature. We have a segregation connected with time and locality and a selection connected with type of gears.

To eliminate the effects of the segregation as far as possible the material had to be collected during the whole season and from a number of localities.

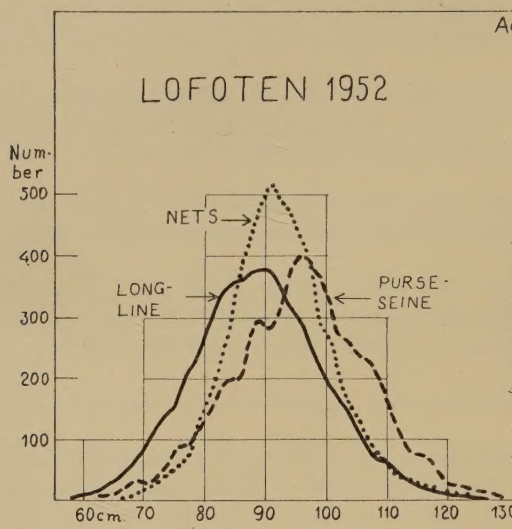
When the material is worked up, the samples from each week are weighted according to the landings in the various harbours.

The selectivity of gears presents even more difficult problems. The sampling of the Lofoten skrei was previously based mainly on longlines because this gear has undergone no alterations

of importance since it was introduced some hundred years ago. The selectivity of the lines is thus probably constant while this is not the case with the gill nets in which the mesh-size is altered from time to time, roughly in accordance with variations in the mean size of the fish.

The picture of the stock presented by the longline samples was a logical one, and the prediction of the stock fluctuations based on the observations were in most cases roughly as accurate as could be expected.

However, in 1950, the purse-seine was introduced in Lofoten, and the catches taken by means of this gear differed considerably from the catches of the older gears as shown in Figure 1.




| Age | P-S | L.L. | N. |
|---|---|---|---|
| 6 | — | 0.10 | 0.09 |
| 7 | 0.62 | 2.18 | 0.72 |
| 8 | 5.14 | 9.07 | 3.98 |
| 9 | 25.45 | 37.15 | 27.22 |
| 10 | 31.16 | 29.85 | 32.95 |
| 11 | 18.47 | 13.33 | 20.30 |
| 12 | 6.17 | 3.72 | 6.91 |
| 13 | 2.54 | 1.20 | 2.00 |
| 14 | 1.77 | 0.54 | 1.21 |
| 15 | 4.62 | 1.18 | 2.13 |
| 16 | 1.39 | 0.62 | 0.71 |
| 17 | 1.15 | 0.40 | 0.37 |
| 18 | 0.68 | 0.29 | 0.75 |
| 19 | 0.61 | 0.26 | 0.55 |
| 20 | 0.10 | — | — |

Figure 1.

A considerably higher number of large fish is taken by the purse-seine than by the nets or lines.

Now, from practical considerations it is unlikely that the purse-seine operates in a significantly selective way. Of course, a horizontal or vertical stratification in the fish layers in respect of size may be reproduced by the purse-seine catches. Thus some catches have been found to consist of 80—90 % of one sex. But such phenomena is a result of a differential behaviour and is not caused by any properties of the gear itself.

If we accept the samples of the purse-seine as representing the true size composition of the stock, we must admit that our previous sampling from the longlines have given us considerably biased length and age distributions of the population, the degree of bias probably varying with the abundance of large fish. The resulting underrating of the number of large fish in the yield predictions has not been of practical importance since, as far as the longlines are concerned, this large fish has not existed at all.

However, the specific selectivity of the longlines must have introduced errors into our calculations of the total mortality rate in the stock of skrei.

We thus see that with increasing knowledge of life history and behaviour new sampling problems have arisen and will probably continue to do so in future also. Sampling will therefore always present some of the main problems in the methods of fishery research.

GUNNAR ROLLEFSEN

# Review of Symposium.

## Origin and Objectives of Symposium.

The importance of fish population studies and their bearing on fisheries conservation has been recognized by the Council for many years, and its meetings have become the main forum for discussion on European progress in this field. This is evidenced by the important part now played by the Council as an advisory body, through its Liaison Committee, to the Permanent Commission of the International Fisheries Convention 1946, and by the already large literature on the subject in the Council's journals.

Hitherto, however, much less attention has been paid in the Council's proceedings to the basic sampling problems which arise in this and other aspects of fisheries work. These problems have grown in importance following the growth of modern population studies and the need for reliable estimates of the vital statistics of the fish populations, and more and greater demands continue to be made on the sampling techniques at the disposal of the fisheries worker.

The symposium held in Paris in October 1954, at which the papers which follow were presented, was designed to promote full discussion of the sampling methods used by European fishery workers and the problems facing them, and so to lay the foundations for the most efficient collection and analysis of data used in population studies. It arose from a recommendation, passed by the North Sea Sub-Committee in Copenhagen in 1953, which read as follows . . . . "that the Consultative Committee be requested to arrange, for the meeting in 1954, a Special Meeting on 'The problems and methods of sampling in the commercial sea fisheries, both demersal and pelagic'". Mr. GUNNAR ROLLEFSEN was invited to convene the meeting and Mr. B. B. PARRISH was appointed Reporter.

In the subsequent planning of the meeting, the organizers felt that its scope should be as wide as possible and should cover not only the specific problems of taking samples of fish from the sea or subsamples from the catch, but also the main objectives of population studies, the basic sampling methods used and the difficulties encountered in sampling fish for population studies generally. These objectives were summarized in a letter, which was circulated to contributors in each nember country and also to Canada, the U.S.A., and F.A.O., as follows:—

(1) To bring together detailed information on the sampling methods used and the difficulties encountered at all stages of the work by European workers engaged in the quantitative evaluation of exploited fish stocks.
(2) To present the results of special theoretical and/or practical investigations in problems of sampling and parameter estimation in fisheries.

In response to this circular were presented fifteen papers, all but one[1]) of which are published in this volume[2]). The papers covered a very wide field within the framework of the symposium, and for convenience they were presented under the following headings:—

(1) Basic sampling theory. Papers Nos. 1, 2, 3 and 4.
(2) Properties of sampling gear and treatment of commercial statistics. Papers Nos. 5, 6, 7, 8 and 9.
(3) Applications of catch sampling data. Papers Nos. 10 and 11.
(4) Sampling methods and problems in various countries. Papers Nos. 12, 13, 14 and 15.

Although some of the papers contained material relevant to more than one of these main sub-divisions, the adoption of this format served to focus attention on the major issues and permitted a comprehensive discussion on each. In view of the prior circulation of most of the papers only a brief summary of each was given at the meeting.

## Review of Proceedings.

1. The importance of the sampling technique, and the magnitude of the difficulties encountered in its application to fish population studies was emphasized by the Convener in his opening address, in which he

[1]) The paper entitled "A method of estimating mortality rates from wartime changes in abundance and structure of fish populations", (Contribution No. 26) by R. J. H. BEVERTON has been withdrawn from publication at the author's request and will appear elsewhere. A brief summary of the method described in this contribution is contained in the paper by BEVERTON and HOLT (Paper No. 10).

[2]) The joint paper by J. A. POPE and R. JONES (Contribution No. 30) is printed as two separate contributions: – Papers Nos. 1 and 4.

outlined the problems of sampling the Norwegian cod fishery at Lofoten. His remarks focussed attention on the sorts of conditions and circumstances which are met in varying degrees in all marine fisheries investigations and which govern the design and execution of all sampling programmes. They are:—

(i) The immense size and variability in space and time of the fish populations themselves.
(ii) The variability in composition, habits, and efficiencies of the fishing units which exploit them.

Both of these primary sets of variables are of importance in determining the ease and accuracy with which the parameters of the fish populations can be estimated from sample data. They emphasize the need for a thorough knowledge by the fisheries worker of the fishery and the gears employed in it and of the practical circumstances in which the samples are taken. Also because of the size and variability of the two basic components of the system, they demonstrate the fundamental importance of statistical theory in the design of the sampling programmes and in the analysis of the resulting data.

2. The rôle of statistical theory and methods was considered in detail in the first four papers. Pope described the basic statistical concepts underlying sampling theory and gave a number of examples of their application to the collection and analysis of fisheries data. He discussed the respective contributions of bias (or systematic error) and random error to the total error arising in population estimates made from sample data. He described a number of sampling systems which are applicable in different circumstances and he outlined the methods of assessing the accuracy of the estimates derived from each. The important relationship between the accuracy of the required estimate and the cost and allocation of the sampling effort was also discussed.

Pope's paper was followed by a contribution from Gulland in which sampling for abundance and age and length composition in the market landings of a fishery was discussed in the light of basic statistical concepts. He took as his main example the English trawl fishery for plaice, and he exemplified the major sources of error (bias and random error) which have to be taken into account in the design of the sampling programme; and he showed how an efficient sampling system could be devised for the investigations in hand. Gulland stressed the need for sampling within each of the strata into which the landings may be divided and the need for the efficient allocation of the sampling effort within and between strata. He drew attention amongst other things to the value of age/length keys in sampling for age and showed that their use reduced the cost of investigation enormously and at the same time provided more accurate population estimates.

These papers were followed by a second contribution from Gulland and one from Jones which discussed the application of statistical theory in the analysis of sample data, and so formed a logical sequel to the earlier papers. Both papers had as their basic theme the use of appropriate statistical transformations on some types of sample data. The need for these arises from the characteristic non-random distribution of fish in the sea which precludes the use of standard statistical analytical tools on the raw data. Gulland discussed the form of the frequency distributions of numbers of fish in replicate hauls and concluded that a transformation to logarithms is generally adequate for most types of data obtained in this way. Jones gave examples of the application of the logarithmic transformations to data used in the estimation of survival rates. He derived expressions from which unbiased estimates of these rates can be calculated from the transformed data, and illustrated their use with data of North Sea and Faroe haddock and northern North Sea plaice.

The contents of these four papers provided the theoretical principles on which sampling programmes can be planned and executed. These are applicable whatever the nature of the investigation or the practical circumstances which confront the investigator, although, of course, they are extremely important in the practical application of these principles. For example, circumstances may make representative stratified sampling of the landings impracticable; or, again, the taking of a truly random sample from a large bulk catch on board ship may be prohibited on practical grounds. Nevertheless, whatever method may have to be devised, it should still, as far as possible, satisfy these basic statistical principles. Otherwise the investigator may be unable to recognize and eradicate the shortcomings of his sampling programme and it will probably be impossible for him to assess the errors in his estimates.

3. The practical circumstances and difficulties which confront the investigator and which govern his choice of sampling programme and methods vary enormously in different fisheries and localities. A number of contributions at the symposium gave examples of particular investigations and discussed the specific problems and difficulties they present in taking representative samples from the sea. One of the most important factors which determine the ultimate accuracy of a population estimate derived from sample data is the extent to which the sampling gear takes a representative sample of the fish population. This factor alone may result in biased population estimates being obtained irrespective of the design and execution of the sampling programme. A knowledge of the sampling efficiency of the different gears employed commercially or those available for special scientific use is fundamental to the effective planning of all sampling programmes.

Specific aspects of this problem were dealt with in contributions by Margetts, Jones and Parrish & McPherson. Margetts and Jones both drew attention to the differences which may arise between samples of fish taken in the same area by different gears, or varieties of rig of a standard gear, and the changes in composition of samples taken in an area

at different times of day. The examples given illustrated the need for extreme care in planning the distribution of the sampling effort in time and space, and in comparing data obtained from different sampling gears. They indicated the importance of preliminary work on the properties of the sampling gear before extensive sampling programmes are undertaken.

Parrish & McPherson classified the causes of sampling inefficiency of a gear into "inherent selectivity", the chief component of which is mesh or hook selection; and "selectivity due to non-uniformity in fish behaviour and habits". They then discussed the relative merits of the drift-net and the trawl as gears for sampling herring and made proposals concerning international co-operation in North Sea herring sampling for the purpose of determining the mortality rate of the North Sea autumn-spawning stock.

4. Contributions which gave a more general account of the rôle of sampling in particular investigations were given by van Cleve & Pruter, Lundbeck and Sætersdal. van Cleve & Pruter discussed the problems of sampling a population of English sole, *Parophrys vetulus* in Puget Sound; Lundbeck reviewed the German programme of market sampling from the deep-sea trawl fisheries in the light of practical circumstances; and Sætersdal described the problems of estimating population parameters of the Lofoten cod stock from sampled data. These papers drew attention to a number of different specific factors which create problems in the design and execution of the sampling programmes and which limit the accuracy of the derived population estimates in different situations.

5. An important aim in fish population studies is to study the impact of a commercial fishery on the exploited fish stock, and to determine the relationship between catch and effort. For this to be accomplished, data are required not only of the composition of the fish stock but also of the activities of the commercial fleet. The importance of statistics of catch and effort, their nature and the immediate needs in current European investigations were considered in the contribution by Beverton & Parrish. They laid particular emphasis on the need for standardized measures of fishing effort, and suggested some appropriate measures for different types of fishing gear. The problem of determining the total effective effort of fisheries conducted by a number of fleets using different gears was discussed in some detail, and a plea was made for the regular collection and publication of effort statistics in standardized units by all European countries, particularly for the North Sea fisheries. While the primary aim should be the collection and publication of a complete census of the catch and effort statistics, the authors drew attention to the possible use of sampling techniques in the collection of statistics where complete censuses cannot be taken.

6. Sampling is a fundamental tool in all branches of fisheries investigations, and the sampling methods used, and the degree of accuracy aimed for will be largely governed by the main objective of each investigation. Therefore in an appraisal of the use of sampling techniques in population studies, it is essential that the main objectives of the investigations and the types of data required should be clearly stated. This important aspect of the symposium was dealt with in a paper by Beverton & Holt, who reviewed in detail the methods which may be used in a variety of circumstances, and the basic data required with each, for estimating two of the most important population parameters,—the fishing and natural mortality rates. They first gave definitions of mortality rates and their mathematical derivation, and then went on to discuss the methods of estimating them from different types of sample data and the possible bias which may arise from various sources. They described the application of some of the methods to southern North Sea plaice data.

7. One of the primary aims of the symposium was to bring together as large a body of information as possible on the methods of sampling now in use by different European countries in their major fishery investigations, so as to facilitate the interchange and interpretation of sample data taken from a fishery by workers from different countries. Unfortunately, this objective was not achieved and only two papers dealt specifically with the sampling methods used. Burd and Gulland outlined those used for the species under detailed investigation in England, and Parrish gave the corresponding information for the herring and haddock investigations in Scotland. Items dealt with in these papers were:— the sources from which samples are taken, the distribution of sampling effort in place and time, the methods of taking individual samples, and the data recorded with each sample.

### Conclusions and Recommendations.

The papers presented at the symposium were followed by a thorough and often lively discussion. It was evident from this and from the contents of many of the papers that progress in population studies was at present hampered by a number of fundamental sampling problems and difficulties which still remain unsolved. Specific items which were considered to warrant special consideration and/or further investigations were:—

(1) The problem of gear selectivity and sampling efficiency.
(2) Difficulties in taking unbiased samples from the single catch or the market landings.
(3) The allocation of sampling effort in space and time in fisheries exploited by a complexity of gears.
(4) The need for statistics of catch and effort as an adjunct to catch sample data in population studies.

Item (4) was considered to be of major importance in the light of the fundamental rôle played by these data in population studies, and the meeting accordingly drafted a recommendation to the Consultative Committee as follows:—

"This meeting is agreed on the need for establishing common standardized units of fishing effort for the various fisheries in the Council's areas and believes a study of suitable units could conveniently be made at an early date by the 'Comparative Fishing Committee'."

Before the proceedings closed, Dr. G. L. Kesteven, Chief of the Biology Branch of the Fisheries Division of F.A.O. addressed the meeting on the world aspects of the problems discussed at the meeting, and Professor G. M. Gerhardsen of the Institute of Economics, Bergen, spoke of the very close liaison which is necessary between the populationist and the fisheries economist because of the interdependence of their respective fields of study.

In his address Dr. Kesteven drew attention to the intention of F.A.O. to arrange a world conference on fishing gear in the near future. The meeting considered this to be of immense importance from many scientific and commercial points of view, and its approval of F.A.O.'s decision was recorded in the meeting's second resolution, as follows:—

"The meeting noted with interest that F.A.O. has in mind to call a meeting during 1956 or 1957 to receive and discuss papers on fishing gear and the reaction of fish to the gear and wished to draw the attention of the Comparative Fishing Committee to this event."

The meeting was closed by the Convener following the adoption of a recommendation that the papers presented should be published *in extenso* subject to the editorship of the Convener and Reporter and that they should be suitably preceded by a review and by an introduction by the Convener.

B.B. Parrish, R. J. H. Beverton.

# 1.

# An Outline of Sampling Techniques.

*By* J. A. Pope
Marine Laboratory, Aberdeen.

## 1. Introduction.

Sampling is the process of selecting a representative part of an aggregate (or population as it is usually called) for the purpose of making comprehensive statements about the nature of the population. Thus the ratio of males to females in the fish population of a lake may be estimated by drawing a representative sample from the total population of the lake and using the observed ratio in the sample as an estimate of the true ratio.

The alternative to sampling is a complete census of the population. When the population is very large considerations of cost and time usually make it impossible to carry out a census and the use of a sample is unavoidable. However, it should be borne in mind at the outset that sampling is not an inferior method of determining population characteristics. In fact, a sample survey possesses a number of advantages over a census. Some of these advantages are:—

(a) Reduction in cost and time: If data are secured from only a small fraction of the population the expenditure of both time and money will usually be smaller than if a complete census had been carried out. In addition, when information is urgently required the use of sampling is quicker both in the collection and the analysis of the material.

(b) More detailed information: The use of trained observers is more practicable in a sample survey than in a complete census and information is likely to be more precise. In addition, it is usually possible in sample surveys to obtain more detailed information. Furthermore, owing to the reduction in the amount of data collected, a finer analysis of the material is possible in sample surveys. Speed in the analysis of a complete census may also be achieved by taking a sample of the data collected.

On the other hand, if detailed information from many sub-divisions of a population is required it may be that a complete census is the only possible solution.

Although only estimates of population characteristics are obtained from samples the accuracy of these estimates is capable of evaluation in well-planned surveys.

Clearly the drawing of a representative portion of the population is an important factor in all sampling investigations. If the population is not homogeneous neither haphazard nor casual selection, and still less deliberate selection, can lead to a good sample.

## 2. Requirements of a good sample.

A sample should be truly representative of the population from which it is drawn. The deliberate selection of units to achieve this is not to be recommended since this approach often leads to appreciable bias.

Bias is a systematic error which is of constant magnitude and which does not decrease in a large population with increasing sample size. The other type of error encountered in sampling is the random error due to chance differences between the units of the population. This latter type of error is referred to as the random sampling error, the sum of this error and the error due to bias being the total sampling error. Whereas the error due to bias does not decrease with increasing sample size the random sampling error is approximately inversely proportional to the square-root of the sample size.

The use of biased estimates is consequently rarely to be recommended since the accumulation and averaging of results may lead to a non-negligible bias. Thus, if $y_1, y_2, \cdots, y_n$ are independent measurements all with constant bias $b$, the bias in the mean is also $b$. The ratio of the bias in the mean to the standard error of the mean is $n$ times that for a single unit and thus may be by no means negligible. Furthermore the presence of bias affects the estimation of confidence limits[1]) since the standard error of the mean does not include the contribution from the bias. In some cases a biased estimate may be easier to handle and may have a smaller variance than the corresponding unbiased estimate. In these cases, especially if the bias is known to be small, use of a biased estimate may be preferable.

A bias which affects all units alike cannot be detected from a sample and represents a serious source of error. In some types of investigations, however, a certain

[1]) See section on simple random sampling.

amount of bias, provided it is reasonably constant, can be accepted. Thus, if we are interested in changes in a population parameter (say) a small bias is of little consequence since its effect will cancel out provided it is constant with time.

Examples of bias in sampling investigations are to be found in Yates (1949).

A further source of error with which we will not be concerned here is that arising from errors of measurement. When errors of measurement are present the value assigned to the $i^{th}$ unit on any particular reading may be assumed to be of the form $y_{ir} = Y_i + \varepsilon_{ir}$ where $Y_i$ is the true measurement of the $i^{th}$ unit and $\varepsilon_{ir}$ the error for that particular reading. In repeat measurements on the same unit the errors are distributed about a true mean which may or may not be zero and which may or may not vary from unit to unit. If this mean is not zero the method of measurement is said to be biased, the bias being positive or negative according as the mean is positive or negative.

### 3. Drawing a sample.

All sampling methods require the sub-division of the population into units called sampling units. Such units may be natural or artificial. Thus, individual fish in a lake are natural units of the total fish population of the lake. The boxes of fish landed by a commercial trawler at a fish market are artificial units of the total catch of the vessel.

The choice of the units to be included in the sample is a matter of supreme importance. The simplest type of objectively selected sample is a random sample; that is, one in which the units are chosen entirely at random. Simple random sampling is a method of selecting $n$ units of the population so that every possible sample of size $n$ has an equal chance of being chosen. In practice a simple random sample may be chosen with the aid of a table of random sample numbers. Such tables, with notes on their use, have been prepared by Fisher and Yates (1954). The random selection of units ensures unbiased estimates of parameters and an estimate of the sampling error. Application of the techniques of statistical analysis is not valid when data have been collected by any other method such as by purposive selection. This would apply, for example, to fish selected from the more accessible boxes in a fish market, there being an implied assumption in the analysis that boxes which are not accessible are similar to boxes which are.

Other sampling designs in which the units are selected at random subject to restrictions will be introduced in succeeding sections.

### 4. Simple random sampling.

Sampling is usually undertaken for the purpose of estimating quantitatively some characteristic of the population. The choice of an estimate is determined mainly by considerations of bias and accuracy. It is not always possible to find an estimate which is both free from bias and of maximum accuracy.

In simple random sampling the arithmetic mean of the sample units is always an unbiased estimate of the true population mean and is of maximum accuracy if the population variates are normally distributed. Moderate departures from normality are unlikely to affect greatly the accuracy although, in sampling from very skew populations, it may be necessary to introduce a scale transformation to obtain a more reliable estimate of the mean.

The accuracy of an estimate is defined in terms of its sampling variance. The relative accuracy of two different estimates of the same quantity is defined as the reciprocal of the ratio of the sampling variances of the two estimates.

If $y_1, y_2, \cdots\cdots, y_n$ is a sample of $n$ units chosen at random from a large population the variance of the population denoted by $\sigma^2$ is estimated without bias by the quantity

$$s^2 = \frac{1}{n-1}\sum_{i=1}^{n}(y_i - \bar{y})^2$$

$$= \frac{1}{n-1}\left\{\sum y_i^2 - \frac{1}{n}\left(\sum y_i\right)^2\right\}$$

where $\bar{y} = \frac{1}{n}\sum_{i=1}^{n} y_i$ is the arithmetic mean. The square-root of the variance is called the standard deviation.

The variance of the mean of a sample of $n$ units is $\sigma^2/n$ and is estimated, without bias, by $s^2/n$. The accuracy of the mean of a random sample from a large population is therefore inversely proportional to the number of units in the sample. The square-root of the variance of the mean is termed the standard error of the mean. The standard error (s. e.) of an estimate is a measure of the average magnitude of the random sampling error in the estimate. Roughly one-third of the actual sampling errors are greater than the s. e. and one-twentieth greater than twice the s. e.

It is sometimes convenient to express the standard deviation of a single unit as a percentage of the mean thereby making it independent of the units of measurement. This quantity is referred to as the coefficient of variation.

**Example 1.** A random sample of 50 herring was drawn from the catch of a herring drifter and the length of each herring measured to the nearest millimetre. The sum and sum of squares of the measurements were 1372.0 cm. and 37731·44 cm.$^2$ respectively. Estimate the true mean length of herring in the total catch. We have

$$\begin{aligned} n &= 50 \\ \Sigma y &= 1372{\cdot}0 \qquad \bar{y} = 1372{\cdot}0/50 = 27{\cdot}4 \\ \Sigma y^2 &= 37731{\cdot}44 \\ (\Sigma y)^2/50 &= 37647{\cdot}68 \\ \Sigma(y-\bar{y})^2 &= 83{\cdot}76 \qquad s^2\ 83{\cdot}76/49 = 1{\cdot}709 \\ &\text{s. e. } (\bar{y}) = (1{\cdot}709/50)^{1/2} = \pm\ 0{\cdot}18 \end{aligned}$$

The arithmetic mean of the sample, 27·4 cm., is an unbiased estimate of the true mean length of the catch. We may be fairly certain that the true mean lies in the range $27{\cdot}4 \pm 2$ (s. e.) $= 27{\cdot}4 \pm 2\,(0{\cdot}18)$, i. e., in the range 27·1—27·8 cm. In fact, only in one case out of twenty (i. e., in 5 % of cases) on average, will the true mean lie outside limits calculated in this way. Such limits are referred to as "confidence limits", the limits here being 95 % confidence limits, since only in 5 % of cases will the true mean lie outside these limits.

## 5. Sampling for proportions.

Frequently we wish to determine the total number, or proportion, or percentage of units in the population which possess some attribute or fall into some defined class. Thus we may wish to estimate the proportion of three-year-old fish in a commercial catch or the proportion of male lobsters on a particular lobster ground.

It is necessary that every unit of the population can be assigned unambiguously to one or other of two classes according as to whether it does or does not possess the required characteristic.

If the total population contains $N$ units of which $A$ possess the characteristic, $C$, under study, the true proportion of units in the population in class $C$ is $P = A/N$. If a simple random sample of size $n$ is drawn from the population and $a$ of these are found to be in class $C$ then

$$p = \frac{a}{n}$$

is an unbiased estimate of $P$. The variance of $p$ is given by $PQ/n$ and is estimated by the quantity

$$s_p^2 = \frac{pq}{n-1}$$

where $Q = 1 - P$ and $q = 1 - p$.

For large values of $n$ ($n > 30$ say) and when $p$ lies between 0·3 and 0·7 it may be assumed for the purpose of setting confidence limits to $P$ that $p$ is normally distributed about $P$ with variance $PQ/n$. For smaller values of $n$ and for values of $p$ outside the range 0·3—0·7 confidence limits may be set using charts devised by Clopper and Pearson (1934) or with the aid of Table VIII in Fisher and Yates (1954).

**Example 2.** In the data of example 1 sex determination revealed that twenty of the herring were males. Estimate the proportion of males in the total catch.

Here we have $p = 20/50 = 0{\cdot}40$ and

$$s_p^2 = \frac{(0.4)\,(0.6)}{49} = 0.0049.$$

With these values of $p$ and $n$ a normal distribution for $p$ may be assumed. Accordingly the 95 % confidence limits for $p$ are

$$0{\cdot}40 \pm 2\,(0{\cdot}0049)^{1/2} \text{ i.e. } 0{\cdot}26—0{\cdot}54.$$

Frequently we are interested in the total number of units which possess the characteristic rather than the proportion of units. That is, we often wish to estimate $A$ rather than $P$. An unbiased estimate of $A$ is given by $N_p$. The variance of $N_p$ is $N^2PQ/n$ when $N$ is known and is estimated without bias by $N^2pq/n - 1$.

**Example 3.** Estimate the total number of males in the catch from which the data of example 2 were obtained.

In this particular case we do not know $N$. However, the drifter landed a total of 20 crans and, from independent sampling of the same catch, it was estimated that there were 1,150 herring to a cran. Hence the estimated total number of males is

$$N_p = (20 \times 1{,}150) \times 0{\cdot}40 = 9{,}200$$

the standard error of this estimate being $\pm$ 1,610, ignoring the fact that $N$ has been estimated. If we take the estimation of $N$ into account the variance of the total is increased by an amount $P^2 \operatorname{var}(N)$.

## 6. Estimation of sample size.

In the planning stage of an investigation an answer must be sought to the question of the size of sample to be taken. Far too often the investigator wastes time and money in either drawing too large a sample in order to "be on the safe side" or in drawing a sample too small to provide any worthwhile information at all.

The size of sample to be taken depends on the desired accuracy of the estimates. This in turn depends on the use to which the results are to be put. It is essential that the investigator have some idea of the amount of error which he can tolerate and also the consequences of errors of different sizes on the decisions to be taken on the basis of the sample results.

The determination of the sample size necessary to achieve a given accuracy in simple random sampling is a relatively easy matter.

**Example 4.** What size of sample should be taken in order to estimate to within 5 % the proportion of females in the landings at a given port over a certain period?

It will obviously be impossible to guarantee 5 % accuracy in any estimate unless the entire landings are sampled. We will therefore assume that the experimenter is willing to accept a one-in-twenty chance of drawing a sample which fails to meet his requirements.

If $P$ is the true proportion and $p$ its estimate then $p$ will lie in the range $P \pm 2\sigma_p$ except for a one-in-twenty chance. Now

$$2\,\sigma_p = 2\sqrt{\frac{PQ}{n}}$$

and this has to equal 0·05. Therefore

$$n = \frac{4PQ}{0{\cdot}0025}.$$

This gives the required size of sample in terms of the unknown quantity $P$. The experimenter, however, has reason to believe that $P$ lies somewhere in the range 0·30 to 0·50. For these values of $P$ we have respectively $n = 336$ and $n = 400$, and accordingly it will be sufficient to take a sample of 400 lobsters.

The sample size necessary to achieve a specified accuracy in the mean of continuous data such as length measurements is found in an analogous manner. If $\sigma^2$ is the true variance of the population, assumed large, then provided the sample size, $n$, is large enough (say greater than 20) the range

$$\bar{y} \pm 2\frac{\sigma}{\sqrt{n}}$$

will include the true mean with probability 0·95. If $e$ is the maximum allowable error the value of $n$ required must be such that

$$e = 2\frac{\sigma}{\sqrt{n}}$$

$$\text{i. e. } n = \frac{4\sigma^2}{e^2}.$$

Here the formula for $n$ involves the true variance of the population and this may be unknown. In many cases, however, data from previous samples are available and these may assist in making intelligent guesses at likely values of $\sigma^2$.

**Example 5.** A sample of herring is to be taken from a particular catch in order to determine the mean length of herring in the catch. Estimate the number of fish required to ensure an error of less than 2 % in the mean.

The mean is known to lie in the range 25—30 cm. and from previous sampling $\sigma^2$ is likely to be around 2·0 cm.$^2$ For these values of the mean we have $e = 0{\cdot}50$ to $e = 0{\cdot}60$. Taking the value of $e$ which will give the largest value of $n$ (viz. $e = 0{\cdot}50$) we have

$$n = \frac{4 \times 2}{(0.50)^2} = 32.$$

## 7. Two-stage sampling.

When sampling from a population made up of a number of primary units each containing a number of smaller units or elements a sample of the primary units may be taken and each selected primary unit subsampled. This method of sampling is referred to as two-stage sampling. In general, when a fixed proportion of the material is to be sampled, decreasing the size of the sampling units leads to an increase in the accuracy of the estimates. This is only to be expected since the elements in any primary unit are likely to be more alike than those from different units.

When a given proportion of the population is to be sampled a decision must be made as to how the sample should be allocated among the primary units. The accuracy of any estimate will not be well determined if only a small number of primary units are included since the standard error of an estimate depends on both the variability within primary units (when these units are not wholly included in the sample) and the variability between primary units. If few primary units are included in the sample the latter component of variance will not be estimated accurately.

In practice the number of primary units which can be included in the sample is often limited by the amount of time (and therefore money) available. Consequently a balance between the degree of accuracy aimed at and the amount of time available has to be sought. In many cases, however, the available time is misspent in drawing large numbers of elements from comparatively few primary units resulting in very inefficient samples.

As an example of two-stage sampling we consider the estimation of the mean length of fish of a given species in the total market landings at a particular time (e. g., on a particular day or in a particular week).

The total landings of fish at a market is usually composed of catches from a number of vessels. The population of fish on the market is therefore made up of a number of large primary units (ships) each unit containing a large number of secondary units or elements (e. g., individual fish or boxes of fish etc.). The fish in each primary unit may be sorted into categories by size but in this section attention will be confined to the case where the individual catches have not been sorted.

Let the total number of ships in the market be $M$ and let $m$ of these be included in the sample. The $m$ primary units may be drawn either with equal probabilities (i. e., at random) or with probabilities proportional to size in terms of the number of elements in the primary units, or to estimated size. In the particular example under consideration it will usually be more convenient to select the $m$ ships with equal probabilities. Although sampling with probabilities proportional to size or to estimated size often possesses desirable advantages over equal probability sampling this method will not be considered further here.

If $n$ fish are chosen at random from each of the $m$ ships, and if $y_{ij}$ is the length of the $j^{\text{th}}$ fish in the sample from the $i^{\text{th}}$ ship the mean length of fish in in the $i^{\text{th}}$ ship is estimated without bias by

$$\bar{y}_i = \frac{1}{n}\sum_{j=1}^{n} y_{ij}.$$

An estimate of the mean length in the total landing is then given by

$$\bar{y} = \frac{1}{m}\sum_{i=1}^{m} \bar{y}_i.$$

This estimate is biased if the primary units are of unequal size although the bias is not appreciable if there is no correlation between the size of unit and the true unit mean and if the number of primary units included in the sample is large. In this and the following sections we will assume negligible bias in $\bar{y}$.

Provided $m/M$ is small (say less than 0·05) the variance of this estimate is given under the above assumption by

$$\text{var}(\bar{y}) = \frac{\sigma_b^2}{m} + \frac{\sigma_w^2}{mn} \qquad (7.1)$$

where $\sigma_b^2$ is the true variance of the unit (ship) means about the overall mean of the population and $\sigma_w^2$ is the true variance (assumed constant from unit to unit) of the elements within any unit about the true unit mean. That is, the variance of $\bar{y}$ is composed of two parts, one ascribable to the variation between the units, the second ascribable to the variation of the elements within the units.

The assumptions involved in deriving (7·1) should be borne in mind.
They are

(i) the primary sampling fraction $m/M$ is negligible,
(ii) the within-ship variance ($\sigma_w^2$) is constant from ship to ship. In practice this is not likely to be strictly true, but unless $\sigma_w^2$ varies widely from ship to ship, formula (7·1) will be acceptable.

One important point which has already been anticipated should be noted, namely, that an increase in $n$ diminishes only the second member on the right of (7·1) while an increase in $m$ decreases both members. That is, the variance of the estimate is decreased by drawing more primary units into the sample.

An unbiased estimate of var $(\bar{y})$ is given by

$$s_{\bar{y}}^2 = \frac{1}{m(m-1)} \sum_{i=1}^{m} (\bar{y}_i - \bar{y})^2$$

$$= \frac{1}{m(m-1)} \left\{ \sum_{i=1}^{m} \frac{\sum_{i=1}^{m} \bar{y}_i^2}{m} \right\}$$

the second form being the more suitable for computation.

**Example 6.** A random sample of five landings of herring was drawn from the total number of landings in a given week and fifty herring were taken at random and measured from each landing selected. The following data were obtained:

| Ship | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| Sum ($\Sigma y$) | 1244·3 | 1324·2 | 1335·4 | 1299·7 | 1270·3 |
| Mean ($\bar{y}_i$) | 24·9 | 26·5 | 26·7 | 26·0 | 25·4 |
| Sum of squares ($\Sigma y^2$).. | 31020·97 | 35127·08 | 35730·30 | 33900·99 | 32358·55 |

Estimate the mean length of herring in the week's landings and its standard error.

The mean length is estimated by

$$\bar{y} = \frac{1}{250}(1244{\cdot}3 + \cdots\cdots + 1270{\cdot}3) = 25{\cdot}9$$

The variance of $\bar{y}$ is

$$s_{\bar{y}}^2 = \frac{1}{5 \times 4} \left\{ (24{\cdot}9)^2 + \cdots + (25{\cdot}4)^2 - \frac{(129{\cdot}5)^2}{5} \right\} = 0{\cdot}113$$

and the required standard error is accordingly $\pm$ 0·34 cm. The 95 % confidence limits for the true mean are 25·2—26·6 cm.

## 8. Effect of modification in allocation.

In order to determine the effect of modifying the allocation of the sample between and within primary units in two-stage sampling separate estimates of $\sigma_b^2$ and $\sigma_w^2$ are required. Once these have been derived from a particular set of observations they may be used for predicting the variance under alternative conditions. In this connection the estimates are useful at the planning stage of new sample surveys.

The estimates of $\sigma_b^2$ and $\sigma_w^2$ are most easily obtained from the analysis of variance[1]) of the sample data. This analysis is shown in the following table.

**Analysis of variance of data from two-stage sample.**

Between primary units

| d. f. | S. of S. | m. s. |
|---|---|---|
| $m-1$ | $n \sum_i (\bar{y}_i - \bar{y})^2 = A$ | $A/m-1$ |

Within primary units

| d. f. | S. of S. | m. s. |
|---|---|---|
| $m(n-1)$ | $\sum_i \sum_j (y_{ij} - \bar{y}_i)^2 = B$ | $B/m(n-1)$ |

The mean squares $A/m-1$ and $B/m(n-1)$ are unbiased estimates of $\sigma_w^2 + n\sigma_b^2$ and $\sigma_w^2$ respectively. Hence their difference divided by $n$ is an unbiased estimate of $\sigma_b^2$. The sum of squares within primary units is most easily obtained by subtracting the sum of squares between primary units from the total sum of squares of deviations from the overall mean, $\sum_{ij} (y_{ij} - \bar{y})^2$ (not shown in table). The process may be illustrated using the data of example 6. The analysis of variance is shown below:—

**Analysis of variance of data from Example 6.**

| | d. f. | S. of S. | m. s. |
|---|---|---|---|
| Between ships .... | 4 | 113·75 | 28·438 |
| Within ships ..... | 245 | 378·62 | 1·545 |
| Total ..... | 249 | 492·37 | |

[1]) For an excellent account of the analysis of variance the reader is referred to Eisenhart (1947).

Denoting the estimates of $\sigma_w^2$ and $\sigma_b^2$ by $s_w^2$ and $s_b^2$ we have

$$s_w^2 = 1{\cdot}545$$

$$s_b^2 = \frac{28{\cdot}438 - 1{\cdot}545}{50} = 0{\cdot}538$$

The estimated variance of the mean is therefore

$$s_y^2 = \frac{0{\cdot}538}{5} + \frac{1{\cdot}545}{250} = 0.1138.$$

This differs slightly from the previous estimate owing to rounding-off.

The estimated variance from a sample of ten ships with twenty-five fish each is

$$s'^2_y = \frac{0{\cdot}538}{10} + \frac{1{\cdot}545}{250} = 0.0600.$$

That is, by keeping the total sample size fixed at 250 and sampling from twice as many ships, the estimated variance is almost halved.

**9. Optimum allocation in two-stage sampling.**

In determining the optimum allocation in two-stage sampling both the degree of accuracy required in the sample estimates and the amount of time available have to be taken into account. The accuracy of the sample mean has already been shown to increase as more primary units are drawn into the sample, but the amount of time involved in moving from unit to unit may set an upper limit to the number of units which can be drawn into the sample.

The total time involved in any survey may be conveniently split up into three separate parts.

(a) The overhead time: This time is more or less fixed irrespective of the method of sampling. It includes, for example, the amount of time involved in drawing up the list of primary units and, when necessary, secondary elements in the population, the time taken in travelling to the primary units from headquarters, and the time required for the subsequent analysis, tabulation, and reporting of the sample data.

(b) Travel time between primary units: This is the time taken in moving from one selected primary unit to the next. It depends mainly on the number of primary units in the sample and their distances apart.

(c) Time at each primary unit: This is the total time taken to deal with the elements within the selected primary units. Clearly this depends on the number of elementary sample units in the primary unit and will vary in proportion to the number of these in the unit.

Ignoring the overhead time, which is more or less independent of the sample, the total time involved in taking the sample may be written as

$$T = t_b m + t_w m n \qquad (9{\cdot}1)$$

where $t_b$ is the time of travel from one unit to the next and $t_w$ is the time required to deal with each element in the sample. This function is perhaps an oversimplification of situations arising in practice but has been found useful on a number of occasions (Gray & Corlett, 1950).

With a time function such as (9·1) the optimum number of elements, $n$, in the units is given by

$$\hat{n} = \frac{\sigma_w}{\sigma_b}\sqrt{\frac{t_b}{t_w}} \qquad (9{\cdot}2)$$

That is $\hat{n}$ increases the greater $\sigma_w^2$ is compared with $\sigma_b^2$ and also the greater $t_b$ is compared with $t_w$. The optimum number of units to be sampled is determined by substituting $\hat{n}$ in either (7·1) or (9·1) according as the accuracy or the total time is fixed.

In determining the optimum allocation a knowledge of $\sigma_w^2$, $\sigma_b^2$, $t_w$ and $t_b$ is necessary.

As an example consider the estimation of the mean length of herring in the total landing of a particular day. We will assume that the total amount of time available for carrying out the sampling is two hours and we will use the estimates of $\sigma_b^2$ and $\sigma_w^2$ found in the previous section[1]). The time taken to select and measure a fish we will assume is twenty seconds and the time required for moving from ship to ship five minutes. This is an oversimplification of the state of affairs usually encountered at a herring port. (See section 10). The optimum value of $n$ is, from (9·2),

$$\hat{n} = 6{\cdot}6.$$

This gives a non-integral number of fish, and the number to be taken in this case should be 6 (Cameron, 1951)[2]). Since the total time is fixed the optimum number of ships is found by substituting $\hat{n}$ in the time function (9·1). This gives

$$\hat{m} = 17.$$

The estimated variance of the mean length of herring from such a sample is, from (7·1)

$$s_y^2 = 0{\cdot}0468.$$

In practice, exact values of the variance components and the time factors will not usually be available and the design derived by this procedure may deviate substantially from the true optimum. Any deviation from optimum allocation will, of course, result in a decrease in the accuracy of the estimate. It is, therefore, always advisable to gauge the breadth of the

[1]) These estimates were derived from data collected over a period of a week but we may assume them to be reasonable estimates of the variance components on a given day.

[2]) As is shown below it is sufficient to choose either $\hat{n} = 6$ or $\hat{n} = 7$. In most cases little error will be committed if we adopt the rule of rounding off $n$ to the nearest integer.

minimum by studying the effect of variations in $m$ and $n$. The following table gives the variance of the mean and the relative accuracy, taking $n = 6$ as standard, for a number of values of $n$, the total time available being fixed at a maximum of two hours.

| $n$ | 2 | 4 | 6 | 9 | 12 | 15 | 20 |
|---|---|---|---|---|---|---|---|
| Variance | 0·0624 | 0·0513 | 0·0468 | 0·0473 | 0·0513 | 0·0534 | 0·0615 |
| Relative accuracy | 0·75 | 0·91 | 1·00 | 0·99 | 0·91 | 0·88 | 0·76 |

For values of $n$ between 4 and 12 inclusive the loss of precision is less than 10 %. Accordingly a certain amount of flexibility in design is allowable. In this example it is only when we deviate widely from the true optimum allocation that a serious loss in precision is incurred.

When the primary sampling fraction $m/M$ is not negligible the expression for the variance of the mean becomes

$$\text{var}(\bar{y}) = \left(1 - \frac{m}{M}\right)\frac{\sigma_b^2}{m} + \frac{\sigma_w^2}{nm}.$$

Thus the contribution to the variance of the between unit component is determined not only by the number of units included but also by the proportion of units included. In particular, if all units are included in the sample (i. e., if $m = M$) the between units component is zero, all contributions to the sampling error arising from the subsampling within units.

## 10. Stratified sampling.

The efficiency of a sample may be increased by the use of stratification. With this method the total population is divided into a number of dissimilar groups, or strata, each stratum being sampled as if it were a separate population.

In stratified sampling when the numbers in the strata are known only the variation within strata gives rise to sampling error. Hence, if it were possible to divide a heterogeneous population into strata within which there was no variation, estimates of population characteristics would be attained without any error. Since the sampling error arises only from variation within strata it is necessary, if an estimate of error is required, that two or more elements be drawn from each stratum.[1])

An example of a stratified population is to be found on a fish market where the landings are sorted into size categories; that is, the fish are stratified by size. Stratification may be employed with advantage in sampling natural waters where the population varies with depth of bottom. Again it may be helpful to employ stratification by time of arrival when sampling herring landings. This procedure allows all fishing grounds to be represented in the sample since, at certain times of the season, the vessels arrive more or less continuously over a period of about six hours, the later arrivals coming from more distant grounds. Special care is of course required when the data are to be used for the estimation of mean length on the grounds. As in previous sections, however, we will confine our attention to the estimation of characteristics pertaining to the population of fish in the market.

As an example of the techniques involved in stratified sampling consider the estimation of the mean length of a particular species in the catch landed by a commercial vessel, the fish being sorted by size before sampling.

Let the number of size categories be $L$ and the total number of fish in the $i^{\text{th}}$ category be $N_i$. Then the total number of fish in the landing is $\sum_{i=1}^{L} N_i = N$. If simple random samples of size $n_1, n_2 \cdots, n_L$ $\left(\sum n_i = n\right)$ are drawn independently from each of the strata an unbiased estimate of the mean length in the $i^{\text{th}}$ stratum is given by

$$\bar{y}_i = \frac{1}{n_i}\sum_{j=1}^{n_i} y_{ij}$$

and an unbiased estimate of the mean length in the whole landing is

$$\bar{y} = \frac{1}{N}\sum_{i=1}^{L} N_i \bar{y}_i.$$

If the same proportion of elements is drawn from each stratum, that is if $n_i/N_i$ is constant from stratum to stratum, the sample mean

$$\bar{y}_s = \frac{1}{n}\sum_{i=1}^{L} n_i \bar{y}_i$$

coincides with $\bar{y}$. In this case each stratum is represented in the correct proportion in the sample and the sample is self-weighting. This method is known as stratification with proportional allocation.

The variance of $\bar{y}$ is

$$\text{var}(\bar{y}) = \frac{1}{N^2}\sum_{i=1}^{L} N_i^2 \frac{\sigma_i^2}{n_i}$$

where $\sigma_i^2$ is the variance within the $i^{\text{th}}$ stratum. An unbiased estimate of $\sigma_i^2$ is (from section 4)

$$s_i^2 = \frac{1}{n_i - 1}\sum_{j=1}^{n_i} (y_{ij} - \bar{y}_i)^2$$

[1]) In special cases approximate estimates of error may be derived when only one element is drawn from each stratum. (YATES, 1949, p. 280).

Accordingly var $(\bar{y})$ is estimated without bias by

$$s_{\bar{y}}^2 = \frac{1}{N^2} \sum_{i=1}^{L} N_i^2 \frac{s_i^2}{n_i}$$

provided $n_i$ is small compared with $N_i$. When $n_i/N_i$ is not negligible it is necessary to take account of this in the estimated variance which becomes

$$s'^2_{\bar{y}} = \frac{1}{N^2} \sum_{i=1}^{L} N_i^2 \left(1 - \frac{n_i}{N_i}\right) \frac{s_i^2}{n_i}$$

$$= \frac{1}{N^2} \sum_{i=1}^{L} N_i (N_i - n_i) \frac{s_i^2}{n_i}.$$

**Example 7.** The following data were obtained from a sample of measurements of the lengths of haddock from the catch of a commercial vessel, the catch being stratified into four groups by size prior to sampling.

| $N_i$ [1]) | $n_i$ | $\sum_j y_{ij}$ | $\sum_j y_{ij}^2$ |
|---|---|---|---|
| 2432 | 152 | 5284 | 185532 |
| 1656 | 92 | 3817 | 158953 |
| 2268 | 63 | 3033 | 146357 |
| 665 | 35 | 2027 | 118169 |
| 7021 | 342 | 14161 | — |

[1]) The quantities in this column are estimates. In this example, however, they will be assumed accurate.

Estimate the mean size of haddock in the catch and its standard error.

The following quantities, obtained by straightforward calculation, are required.

| $\bar{y}_i$ | $N_i \bar{y}_i$ | $s_i^2$ | $s_i^2/n_i$ | $N_i^2 s_i^2/n_i$ |
|---|---|---|---|---|
| 34·763 | 84544 | 12·21 | 0·0803 | 474900 |
| 41·489 | 68706 | 6·47 | 0·0703 | 192800 |
| 48·143 | 109188 | 5·48 | 0·0870 | 447500 |
| 57·914 | 38513 | 22·85 | 0·6529 | 288700 |
| | 300951 | | | 1403900 |

$$\bar{y} = 300951/7021 = 42{\cdot}9$$

$$s_{\bar{y}}^2 = 1403900/(7021)^2 = 0{\cdot}0285$$

$$\text{s. e. } (\bar{y}) = \pm 0{\cdot}17.$$

The 95 % fiducial limits for the true mean of the catch are therefore 42·6—43·2 cm.

Errors in the stratum sizes affect both the estimated mean and the standard error of the mean. If estimates $\hat{N}_i$ of the true stratum sizes are used, the mean

$$\bar{y} = \frac{1}{\hat{N}} \sum \hat{N}_i \bar{y}_i$$

where $\hat{N} = \sum \hat{N}_i$ is biased. In addition, the true variance of the estimated mean is inflated roughly by an amount equal to the square of the bias. Accordingly the estimated variance should include a component due to errors in the $\hat{N}_i$'s to allow for this. If some knowledge of the variance of the $\hat{N}_i$'s is available the magnitude of the contribution from the bias to the standard error of the mean may be gauged (Cochran, 1939).

## 11. Allocation in stratified sampling.

If the total size of sample, $n$, is fixed and no consideration of time factors is involved, the variance of the estimated mean is a minimum when the sample is allocated with $n_i/N_i$ proportional to the within-strata standard deviation of the elements, $\sigma_i$. (Neymann, 1934). This means that a larger sample is required in a highly variable stratum.

In many cases the true within-strata standard deviations will be unknown and when these are estimated true optimum sampling will only be approximately realised. However, as a rule, the variance is not very sensitive to deviations from optimum allocation.

The magnitudes of the within-strata standard deviations may be estimated from previous data where these are available and not out of date, or by preliminary sampling of the population. Thus, in sampling the landings of commercial vessels which have been stratified by size the use of estimated standard deviations obtained from previous surveys would seem to be adequate in view of the consistency of the method of stratification employed. The within-strata standard deviations will, of course, alter with changes in the total number of size categories involved but this presents no difficulty.

In general the use of stratification as compared with simple random sampling will result in increased accuracy in the estimates. The decrease in the variance of estimates obtained with optimum sampling arises from the elimination of differences between stratum means and of the effect of differences between the within-strata standard deviations. In the case of landings stratified by size it is as well, therefore, to take advantage of the stratification when estimating mean length or any quantity correlated with length.

## 12. Cluster sampling.

In practice it is often more practicable and time saving to draw a sample in groups rather than to select individuals at random. This is usually the case in sampling fish landings when, for example, it is common practice either to select fish from the same box rather than select at random from all the boxes, or to take the first twenty fish (say) from a random scoopful. This method of sampling is referred to as cluster sampling. If the elements within clusters are homogeneous this technique leads to a loss of efficiency compared with unrestricted random sampling. On

the other hand when the clusters are composed of elements which are very heterogeneous the use of cluster sampling leads to a gain in efficiency.

The relationship between the variances of an estimate obtained from a random sample and a cluster sample of the same size may be expressed conveniently in terms of the intraclass correlation coefficient, $\varrho$. This quantity is a measure of the degree of homogeneity of elements within clusters with respect to some characteristic or measurement. When measurements within clusters are relatively homogeneous the intraclass correlation coefficient between measurements within clusters will be near to $+1$. Conversely if the measurements within clusters are relatively heterogeneous the intraclass correlation coefficient will be near zero and may even be negative.

This concept may be illustrated by considering the estimation of the proportion of three-year-old fish in a commercial catch. If most of the fish in some boxes are three-year-olds and most of the fish in the others are older than three years the variance between boxes of the proportion of three-year-old fish will be large and the intraclass correlation within boxes will be near $+1$. In this case a sample of one box will give a poor estimate of the proportion of three-year-olds in the landing.

On the other hand if the fish in each box were selected at random from the total catch the age composition in any box will correspond to that obtained by drawing a completely random sample from the catch. In other words, the variance of the estimated proportion of three-year-old fish obtained from a cluster sample would be the same as that from a random sample. The intraclass correlation here is zero.

Finally, if the proportion of three-year-old fish is the same in every box the variance between boxes will be zero. A sample of all the fish in one box will provide complete information on the age composition for we have only to sample one box to get the exact proportion of three-year-old fish in the catch. In this situation the intraclass correlation is negative.

If a sample of $m$ clusters with $n$ elements in each is drawn the variance of the estimated mean per element is

$$\text{var}(\bar{y}) = \frac{\sigma_b^2}{m}$$

where $\sigma_b^2$ is the true variance between cluster means. This may be written as

$$\frac{\sigma^2}{mn}\left\{1 + (n-1)\varrho\right\} \qquad (12{\cdot}1)$$

where $\sigma^2$ is the variance of a single element and $\varrho$ is the intraclass correlation coefficient between elements within clusters.

The corresponding variance for a completely random sample of $mn$ elements is

$$\text{var}(\bar{y}') = \frac{\sigma^2}{mn}$$

which is the same as (12·1) apart from the factor $\left\{1 + (n-1)\varrho\right\}$. Clearly, if $\varrho$ is positive this factor is greater than 1 and cluster sampling is less accurate than unrestricted random sampling. When $\varrho = 0$ the two variances are the same and cluster and random sampling are of equal efficiency. In the extreme case when $\varrho$ assumes its minimum value, $-1/(n-1)$, each cluster is a replica of the population and var $(\bar{y})$ is zero.

The relative efficiency of the two types of sampling may be estimated using data from a cluster sample. If $m$ clusters each of $n$ elements have been sampled the analysis of variance of the results is

**Analysis of variance of data from cluster sample.**

| | d. f. | S. of S. | m. s. |
|---|---|---|---|
| Between clusters.. | $m-1$ | $n_i \sum (\bar{y}_i - \bar{y})^2$ | $B$ |
| Within clusters ... | $m(n-1)$ | $\sum_i \sum_j (y_{ij} - \bar{y}_i)^2$ | $W$ |
| Total ..... | $mn-1$ | $\sum_i \sum_j (y_{ij} - \bar{y})^2$ | $T$ |

Here $B$ is an unbiased estimate of $n\sigma_b^2$ and $W$ an unbiased estimate of $\frac{n}{n-1}\sigma_w^2$ where $\sigma_w^2$ is the variance of elements about the mean of the cluster to which they belong. Writing $F = B/W$ the intraclass correlation coefficient is estimated by

$$r = \frac{F-1}{n+F-1}$$

and the efficiency of cluster sampling relative to unrestricted random sampling by $\left\{1 + (n-1)r\right\}^{-1}$.

It should be noted that the total mean square is a biased estimate of the variance of an element from a random sample $(\sigma_b^2 + \sigma_w^2)$, the bias being positive when $\varrho$ is negative and negative when $\varrho$ is positive. This bias may be removed by estimating $\sigma_b^2 + \sigma_w^2$ from

$$\left\{(mn-1)T + B\right\}/mn.$$

## 13. Concluding remarks.

The material contained in the preceding sections gives an account of the methods of planning and analysing the results of sample surveys. The examples which have been given to illustrate the techniques are in almost all cases oversimplifications of the types of problems encountered by fishery scientists. Each particular investigation will invariably call for a combination of various designs and analytical techniques. This occurs, for example, in market sampling where it is usually necessary to introduce two-stage sampling with stratification occurring at the second stage and perhaps cluster sampling within strata. Furthermore it will frequently be the case that estimates of a number of characteristics are required such as length,

age, sex, etc. The optimum sampling designs for all characteristics on which information is sought will hardly ever coincide and it will usually be necessary to make some compromise. The basic theory presented here, however, should be sufficient to deal with most types of investigations.

It is important to realize that no hard and fast rules can be laid down for collecting and analysing sample data except in so far as to say that some form of probability selection must be employed in choosing the elements which are to be included in the sample, and the sample designed to reduce as far as possible the variance of the estimates. Each investigation presents its own problems and peculiarities calling for modifications and alterations of techniques. Suitable sampling designs can be arrived at only after sufficient information on variances and time factors has been made available. For this reason the results of all sample surveys should be preserved, for all surveys provide some information on variances and time factors which may be useful at the planning stage of later investigations.

## 2.

# The Study of Fish Populations by the Analysis of Commercial Catches.

### A Statistical Review.

*By* J. A. Gulland[1])

Statistically, the study of fish populations from an analysis of commercial catches may be regarded as two successive sampling processes: first, the commercial catch forms a sample from the total population and second, a sample is taken from the catch for scientific examination, e. g., length measurement or age determination. In this paper these two processes will be analysed from the statistical viewpoint, in order to find a method of sampling and subsequent analysis giving the least variance and bias. Roughly speaking, the *variance* is the scatter, about their mean value, of successive estimates of some quantity, e. g., the length of the fish in the catch. The *bias* is the amount whereby this mean value of the estimates differs from the true value. Thus the variance can be readily detected in any series of observations, while bias may be difficult to detect. The fact that repeated samples give very much the same answer can be no guarantee that there is no bias, or even that the bias is small.

In a particular sampling system, the variance will be approximately inversely proportional to the amount of sampling, but bias cannot be reduced by increasing the amount of sampling, but only by using a correct sampling system. The "best" system of sampling and subsequent analysis, judged on a statistical basis, will be that which is as far as possible free from bias, and which gives the smallest variance for a given sampling effort. Looked at another way, it will require the smallest amount of sampling to reduce the variance to some desired level. The sampling pattern giving the smallest variance for one estimate will not necessarily be that giving the smallest variance for some other estimate; for instance the best sampling design to find the average age may not be the best for finding the ratio of males to females. Therefore the choice of sampling pattern depends, possibly quite critically, on the information ultimately required. In population work the most important estimates are for the fundamental parameters: growth, natural and fishing mortality and recruitment. Of these, the most difficult to estimate, and the most liable to sampling errors, are the mortalities. The methods of estimating them, and the type of information required, are discussed more fully by Beverton and Holt (1955). The most useful estimates are in the form of indices of abundance for each age-group; i. e., numbers proportional to the total numbers of fish of that age in the sea, the coefficient of proportionality being constant from year to year. Less useful is the relative age composition during each year; e. g., percentage age composition. It may not be generally realized that a *faute de mieux* estimate of mortality may also be made, when age determinations are not available, from similar data on length composition. Beverton and Holt also discuss methods of estimating fishing mortality alone, which do not directly need sampling of the commercial catch in the manner described here, though catch sampling is needed for estimation of total mortality.

For the ultimate purposes of this paper, therefore, the quantities for which estimates will be made, and bias and variance calculated, will be indices of abundances for each age- and length-group. As an intermediate step, but also intrinsically very important, the numbers of fish of each age and length group landed by the commercial fishery will be estimated. This will also give a relative age and length composition. The latter problem will be discussed in the first part of this paper; the second part will deal with estimation of the composition of the stock.

[1]) A fuller exposition of this subject is in press. (Gulland, 1955).

**Sampling of the commercial catch.**

The direct sampling of the commercial catch for length and age composition presents in general a straightforward statistical problem, and the variance may be readily calculated. Bias may arise both in the choice of the section of the catch from which to sample, and the choice of fish to be measured within this sample. After the fish are landed and sold, a single ship's catch is likely to be divided among several different merchants. Each will tend to buy that size of fish which is particularly suited to his requirements, so that measurements of fish taken at any particular merchant are unlikely to be representative of the whole catch. Therefore, to avoid bias from this cause, the samples have to be taken directly from the landings, before the catch of each ship is split up. Even then bias may occur when the catch is divided into two or more categories, on a basis of size or condition of the fish, unless a sample is taken from every category. This is obvious when the basis of categories is size, but it is also true when the catch is divided according to the condition of the fish. For instance at Lowestoft, the main categories for plaice are "large", "medium" and "small", but particularly after the spawning season, thin and damaged fish are sorted out. These last seldom amount in weight to more than a few per cent. of the total landing, but may contain half the biggest and oldest fish. Obviously the number of old and big fish would be seriously under-estimated if the three main categories were taken as representative of the whole catch. This is illustrated in the table below.

In this hypothetical, but yet realistic sample, the weight of the thin fish is barely 1 % of the whole, but they comprise nearly a quarter of those fish above 50 cm.

The choice of sample within a landing category is probably unimportant, the difference in composition between different parts of the same category being likely to be small. If such a difference does exist, it is likely to be most marked between the first and last fish landed, i. e., probably between the last and first fish caught. During one month at Lowestoft two samples were taken from the same category off a number of different ships, the samples comprising respectively the first and last batches of fish landed. No significant difference was found between samples from the same ship, though there was considerable differences between ships.

Bias may also arise through personal selection within the sample taken for measuring. If only a fraction of the fish available for selection are picked up and measured, this fraction will, for most people, contain rather too many big fish. Often too, the top few fish in a box have been selected and put there to impress the buyers. For instance, a sample of 50 fish picked carelessly off the top of a box of small plaice (containing altogether some 300 fish) may have an average length some half-centimetre greater than the rest. This is an important difference when the whole length range is only a few centimetres. This bias is easily avoided by measuring all the fish in a box, which makes selection impossible, or by taking all the fish from one side, so that the sample measured consists of all the fish originally to one side of the box, and again selection is impossible or difficult. This same problem arises in sampling a haul by a research vessel. Here again it is best, if at all possible, to take the whole catch as a sample. But, because there may be a tendency for the big fish all to go to the side, even taking all the fish in one part of the catch may give an unrepresentative sample. Such selection will be most likely to occur when the size range of the fish is great. For instance it is more probable in a sample of cod, where the biggest fish may weigh 10 times more than the smallest, than for herring where the biggest may be only twice the size of the smallest.

The variance in the length distribution may often be reduced by a suitable choice of sampling method. In a paper read at the Meeting of the Council in 1953, it was shown that the variance using a large number of small samples was considerably less than when the same number of fish were measured in a few big

**Table 1. Hypothetical Example of Catch by Categories of a Lowestoft Trawler.**

| | | Large | Medium | Small | Thin | Total |
|---|---|---|---|---|---|---|
| Weight landed (stones) | = A | 30 | 100 | 480 | 10 | 620 |
| Weight measured „ | = B | 10 | 5 | 3 | 10 | .. |
| Raising factor | = A/B | 3 | 20 | 160 | 1 | .. |

| | Length Group (cm.) | 25—29 | 30—34 | 35—39 | 40—44 | 45—49 | 50+ | Total |
|---|---|---|---|---|---|---|---|---|
| Number measured | Large C | — | — | — | 16 | 33 | 15 | 64 |
| | Medium D | — | 2 | 47 | 27 | — | — | 76 |
| | Small E | 26 | 41 | 8 | — | — | — | 75 |
| | Thin F | — | — | 7 | 15 | 14 | 14 | 50 |
| Number landed | Large C×3 | — | — | — | 48 | 99 | 45 | 192 |
| | Medium D×20 | — | 40 | 940 | 540 | — | — | 1,520 |
| | Small E×160 | 4,160 | 6,560 | 1,280 | — | — | — | 12,000 |
| | Thin F×1 | — | — | 7 | 15 | 14 | 14 | 50 |
| | Total | 4,160 | 6,600 | 2,227 | 603 | 113 | 59 | 13,762 |
| | Total less thin | 4,160 | 6,600 | 2,220 | 588 | 99 | 45 | 13,712 |

**Table 2. Hypothetical Example to show the Use of Categories to obtain total Length Distribution from that of a single Ship.**

| | | Large | Medium | Small | Thin | Total |
|---|---|---|---|---|---|---|
| Total weight landed | A | 750 | 1,500 | 3,840 | 110 | 6,200 |
| Weight landed by sampled ship | B | 30 | 100 | 480 | 10 | 620 |
| Raising factor | A/B | 25 | 15 | 8 | 11 | 10 |

| Length (cm.) | | | 25—29 | 30—34 | 35—39 | 40—44 | 45—49 | 50+ | Total |
|---|---|---|---|---|---|---|---|---|---|
| Number in sample | Large | C | — | — | — | 48 | 99 | 45 | 192 |
| | Medium | D | — | 40 | 940 | 540 | — | — | 1,520 |
| | Small | E | 4,160 | 6,560 | 1,280 | — | — | — | 12,000 |
| | Thin | F | — | — | 7 | 15 | 14 | 14 | 50 |
| | Total | G | 4,160 | 6,600 | 2,227 | 603 | 113 | 59 | 13,762 |
| Total number landed (i) (ii) | Large | C×25 | — | — | — | 1,200 | 2,475 | 1,125 | 4,800 |
| | Medium | D×15 | — | 600 | 14,100 | 8,100 | — | — | 22,800 |
| | Small | E×8 | 33,280 | 52,480 | 10,240 | — | — | — | 96,000 |
| | Thin | F×11 | — | — | 77 | 165 | 154 | 154 | 550 |
| | Total | G×10 | 41,600 | 66,000 | 22,270 | 6,030 | 1,130 | 590 | 137,620 |
| | Sum of categories | | 33,280 | 53,080 | 24,417 | 9,465 | 2,629 | 1,279 | 124,150 |

samples. For instance, for medium plaice, the same accuracy can be obtained with a quarter the effort by taking samples of 50 fish in each sample, than with fewer samples of 400 fish in each sample. This result, indicating an upper limit to the efficient size of sample of around 50 fish, has been found to be applicable to all species of fish (cod, plaice and hake) for which it has been tested.

The variance may also be reduced, and possible bias eliminated, by stratified sampling. That is, the total landings may be divided up into a number of different strata, e. g., by ports, method of capture, time of landing etc. Samples are taken from each separate stratum and estimates made of its length composition. These separate estimates are then combined to give the length composition of the total landings. The more dissimilar the strata, the greater is the benefit gained by using stratified sampling.

The most advantageous stratification is the division provided by market categories based on size. The estimate of the length distribution of the catch of the vessel which is sampled is, of course, obtained by the use of stratified sampling (see Table 1), but the estimates for the landings of all vessels may or may not involve the use of categories. The two methods are demonstrated in Table 2, which shows the further analysis whereby the catch of one ship, given in Table 1, is raised to give the total catch of all ships.

Ignoring categories, the total length composition is obtained by multiplying the catch of the sampled ship (row G) by the ratio of total catch to sample catch. The result is given in the last but one row. The composition of the individual categories may be calculated, and then added together, to give the sums in the last row. Because the sampled ship contained relatively more of the category "small" and less "large", it is to be expected that, by ignoring categories, the numbers in the smaller length groups would be over-estimated and those in the larger sizes under-estimated. This can be seen at once to be so, by comparing the totals in the last two rows. The gain in accuracy by this use of categories is considerable. The variance of the Lowestoft plaice measurements, using this method, is about one quarter of that without stratification.

Besides stratification by market categories, when these are sufficiently well defined to be applicable, the English landings are also divided by ports and by month of capture. While these stratifications do not reduce the variance to anything like the same extent as does the use of market categories, they are of great importance in eliminating possible bias. This is because it is much easier to take a truly random sample at one port for a short period than from landings at several ports and extending over a long period. Thus, without stratification, one section of the landings is very likely to be over-represented in the samples. For instance more plaice from North Sea trawlers are landed at Grimsby than at Lowestoft; at the same time, for practical reasons, more fish can be measured at Lowestoft than at Grimsby. Thus, the Lowestoft landings are over-represented in the samples; moreover, they contain rather smaller fish, so that without stratification by ports, there would be a bias towards under-estimating the average size of fish.

For much theoretical population work the knowledge of the age-composition is rather more important than that of the length composition. Fortunately, the age of most commercial fish in European waters can be determined from scales or otoliths with a fair degree of accuracy. Apart from any definite errors in the age determinations, a definite bias can be introduced by ignoring in the calculations those otoliths or scales which are difficult, but not impossible, to read. These will usually be the older, slow growing fish, and their omission would give a bias towards under-estimating the average age. The degree of this bias for the North Sea plaice age determinations is indicated in Table 3. This is based on the regular

**Table 3. Average Age of Lowestoft and Grimsby Otolith Samples, showing difference between doubtful and definite Otoliths.**

| Length group (cm.) | Number of fish | | | Average age | | |
|---|---|---|---|---|---|---|
| | Doubtful | Definite | Total | Doubtful | Definite | Total |
| 25—29... | 22 | 338 | 360 | 4·4 | 4·1 | 4·1 |
| 30—34... | 27 | 332 | 359 | 5·7 | 5·2 | 5·2 |
| 35—39... | 46 | 313 | 359 | 7·6 | 6·1 | 6·3 |
| 40—44... | 70 | 170 | 240 | 8·8 | 7·0 | 7·5 |
| 45—49... | 99 | 139 | 238 | 11·0 | 8·7 | 9·6 |
| 50—54... | 120 | 117 | 237 | 12·2 | 10·9 | 11·6 |
| Total .... | 384 | 1409 | 1793 | 9·8 | 6·1 | 6·9 |

plaice sampling at Lowestoft, for which an age is attached to every otolith read, those which are difficult to read being recorded as doubtful.

Out of the 1793 otoliths examined, a little under a quarter, (384) were recorded as doubtful, but the proportion of doubtfuls varied greatly with the size of fish. Only 5 % of the smallest (25—29 cm.) length group, but over half the biggest (50—54 cm.), were doubtful.

Taking all the otoliths together, the average age of the doubtful group was nearly four years greater than that of the definite group, and their omission would apparently reduce the average age from 6·9 to 6·1 years, a very considerable degree of bias. This difference is partly due to the doubtfuls, within any length group, being rather older than the definites, but also to the average size being considerably greater: 44·8 cm. against 36·8 cm. for the definite group. The latter difference must be real, and cannot be the effect of any errors in the age determination of the difficult otoliths. The former difference may either mean that the age of the slower growing fish is harder to determine, which is quite likely, or that there is a tendency to over-estimate the age when the otolith is difficult to read.

Because they are likely to be perhaps a year or so out either way, the inclusion of doubtful otoliths will tend to blur the differences between adjacent year-classes. The otoliths belonging to a strong year-class, but recorded in error as belonging to an adjacent, weak year-class will not be balanced by the otoliths in fact belonging to the weak year-class, but recorded as belonging to the strong year-class. Therefore when there is a particular interest in the comparative strengths of year-classes rather than in a correct overall age distribution, it may be better to risk a bias in the age composition, and omit the doubtful otoliths.

Age composition may be obtained by sampling directly for age in exactly the same way as for length distributions. However, because the length of a fish gives a good guide to its age, and also many length measurements may be done as quickly as one age determination, the age composition may be often most easily obtained from a large number of length measurements, and a relatively few age determinations, as has been described and used by FRIÐRIKSSON (1934) and others. The practical advantages of the method would be expected to be greatest when there was a big variation in length composition between successive samples, and when the fish grow quickly and fairly uniformly. Both these conditions are satisfied in many commercial fisheries, and the use of an age/length key may, for a given amount of sampling, more than halve the variance of the age distribution.

Possible bias in the method is small, assuming the length data to be unbiased. It could arise, not through sampling too many fish of one age but only by sampling too many of one age within a single length group, which seems unlikely to happen. Any tendency to include too many big, or small, fish in the sample for age, is immediately corrected for. This can be taken advantage of to give better accuracy for the older and scarcer fish. In a random sample, one or two length groups, and a few age-groups, will usually predominate, and the abundance of these ages will be known reasonably accurately. Conversely the older age-groups will occur only rarely, and their abundance will be only poorly determined. It is often best to know the abundance of most year-classes about equally well, and this may be achieved by using an age/length key and taking samples for age determination not randomly, but so as to give about equal numbers in each length group.

Because the age/length key depends only on the growth characteristics of the fish which are liable to be less variable than the sample age composition, it does provide a more or less reliable method whereby results gained from age and length studies on one section of the catch or population may be extended to a section for which length measurements only are available. For instance, market measurements of the commercial catch may be converted to an age composition by means of otolith samples taken from the catch of a research vessel. Again, when several countries are fishing one area, it may happen that age and length measurements may be made by only one country, but that length measurements are made by several. For instance, at present only length measurements are being made on samples of the catches of cod from Iceland landed by English trawlers. For at least a first approximation, age samples from Icelandic catches from similar areas could be used to form an age/length key applicable to the English catches, and thus to determine the number of fish of each age-group in the English landings.

### The commercial catch as a sample of the fish population.

In considering the commercial catch as a sample of the natural population of a species at the ages liable to capture, it is useful to distinguish between sampling for density or abundance, and sampling for structure, i e., length or age composition. In assessing the density, each haul may be considered as giving a sample of the density of the fish at that position, and we will suppose that for a given haul:—

$$d_i = cD_i$$

where $d_i$ = catch in $i^{th}$ haul

$D_i$ = density of fish at the position of $i^{th}$ haul

$c$ = constant

that is, a single haul will take, on the average, a fixed proportion of the fish present. This is probably true for such gears as trawls and seines, though other kinds of gear such as long-lines, may become saturated in heavy fishing, e. g., when most of the hooks are occupied, and take a smaller proportion when the density is high. However, on our assumption, when the results of several hauls are combined, we have:—

$$\sum d_i = \sum cD_i$$

or, taking the mean

$$\begin{aligned} \overline{d} &= c\overline{D} \\ &= c'D \end{aligned}$$

where $\overline{d}$ = mean catch per haul, i. e. catch per unit of effort

$\overline{D}$ = average density of fish at the fishing positions

$D$ = average density of fish over the whole region

$c'$ = constant.

The constant $c'$ will be different from $c$ (usually larger), because fishing will usually be done where the fish are most abundant, so that the average density at the fishing positions will be greater than the average over the whole area. As we are only attempting to find a number proportional to the density, or abundance, it is not necessary, or indeed possible, to know the value of $c'$. Strictly then, bias will be impossible, but an analogous effect will be steady long-term changes in the average value of $c'$ particularly from year to year. Possible sources of variation in $c'$ include:—

(i) Random haul-to-haul variations.
(ii) Weather.
(iii) Behaviour of the fish.
(iv) Skill of the fishermen.
(v) Changes in the distribution of the fleet in space and time.
(vi) Changes in the power and size of the ship, type of gear etc.

The first of these, though it may be large and give a coefficient of variation of say 60 % for a single haul, becomes negligible when the number of hauls is large. For instance, in the mean of 10,000 hauls —not a very large number in relation to the activities of a whole fleet—a coefficient of variation of 60 % for a single haul, is reduced to only 0·6 %. Thus the variance from this cause may be reduced to a reasonable value by having catch per unit effort figures for possibly only a small sample of the fleet. Similarly the effects of weather, when averaged over a whole year, may be expected to be small, though possibly important over smaller periods of time. Changes in the behaviour of the fish, particularly for lines or gill-nets, which depend on the fish catching themselves, can have a large effect particularly between different seasons of the year. However, the behaviour is likely to be the same at a given season, from one year to the next; also changes in behaviour are liable to be difficult to detect and estimate and will not be considered further in this paper. Similarly the skill of the fishermen will be assumed to be constant.

The most important source of variation of $c'$ is formed by changes in the fishing power of the ships or gear, as these may be considerable; and, at least as important, they are likely to change consistently and steadily from year to year. For instance, between 1923 and 1927, the introduction of the Vigneron-Dahl gear raised the fishing power of steam trawlers by some 50 % (Bowman, 1932) and thus, relative to the period before 1923, the density of fish after 1927, as estimated from the catch per hour of steam trawlers, is over-estimated by 50 %. Similar changes in the power of ship, have been taking place over a longer period in the English distant-water trawler fleet. To a fair approximation, the fishing power of these trawlers is proportional to their gross tonnage. In 1930 the average tonnage of newly built distant-water trawlers was some 350 tons; this increased to 450 tons in 1947, and to some 600—700 tons now. The effort statistics on which the catch per unit effort figures are based must therefore be calibrated.

The relation between $c$ and $c'$ and hence the value of $c'$ will depend on the relative distributions of the fish and the fishing. This is best discussed in two parts. First, on a single fishing ground, there will be a difference between the average density at the actual positions of the ships, and over the whole fishing ground, and secondly there will be a difference between the average density on the fishing grounds, weighted by the amount of fishing on each, and the average over the whole region inhabited by the stock. The first of these is dependent on the ability of the fishermen to find small local concentrations of fish, and is largely a matter of skill, though it may be affected by such items of gear as radar, or Decca, for more accurate navigation, or the echo-sounder for better location of the fish. The second difference, which may be termed the concentration, will depend on the decision of the fishermen on which ground to go to, whether, for instance, to go a long way from port for good catches, or to stay nearer port for poorer catches. It is likely to be particularly important when two or more species inhabit more or less separate areas within the same region, e. g., haddock and plaice in the North Sea. Here a real increase in the density of haddock might mean more ships would fish for haddock than for plaice. They would thus leave the plaice area; the catch of plaice, for the

same total North Sea effort would drop and the apparent density of plaice would decrease.

The effect of varying distribution of fishing on one fishing ground is difficult to estimate, but the effect of concentration can be estimated and allowed for, provided sufficiently detailed information is available.

Suppose the whole region is divided up into a number of small sub-areas, in each of which the catch and effort are known. Then we can write, for the $i^{th}$ sub-area:—

$$D_i = \frac{1}{c} d_i$$

where $D_i$ = density in $i^{th}$ sub-area
$c$ = constant
$d_i$ = catch per unit effort in $i^{th}$ sub-area;

assuming that the effects of non-uniform distribution within the area may be taken as constant.

Then if $N_i$ = total numbers of fish in $i^{th}$ sub-area
$a_i$ = area of $i^{th}$ sub-area

and similar symbols without the sub-script denote the values for the whole region, then

$$N = \sum N_i$$
$$N_i = a_i D_i$$
$$N = aD$$
$$\therefore aD = N = \sum a_i D_i$$
$$= \sum a_i \cdot \frac{1}{c} \cdot d_i$$
$$\therefore D = \frac{1}{c} \frac{\Sigma a_i d_i}{a}$$

i. e., the density index is the weighted mean of the catch-per-unit-effort in each sub-area, the weighting factors being the size of the sub-areas. This equation is effectively the same as that developed by BEVERTON and HOLT (in press) and BEVERTON and PARRISH (1955) for the effective overall fishing intensity $\tilde{f}$. For if $f_i$ and $Y_i$ are intensity (i. e., effort per unit area) and catch in the $i^{th}$ sub-area, respectively, and $Y$ the total catch,

$$\frac{Y}{a\tilde{f}} = cD = \frac{\Sigma a_i d_i}{a} = \frac{1}{a} \sum a_i \frac{Y_i}{a_i f_i}$$
$$\therefore \tilde{f} = \frac{Y}{\Sigma Y_i / f_i}.$$

A numerical value for the concentration is given by the ratio of the simple fraction total catch divided by the total effort to the weighted index of density.

That is, concentration $= \frac{c'}{c} = \frac{ad}{\Sigma a_i d_i}$

or if there are $n$ sub-areas, each of equal area,

$$\text{concentration} = \frac{nd}{\Sigma d_i}.$$

This ratio has been calculated for British steam trawlers fishing in the central North Sea (region IVb), west of 4° E., for the years 1947 to 1952. The sub-areas used were the usual statistical rectangles, approximately 30 miles square. For plaice the ratio has varied between 1·64 in 1948, and 1·42 in 1950, a decrease of 13 %, and for haddock between 0·61 in 1947 and 0·86 in 1949, an increase of 41 %. While for plaice, the preferred species in this region, the ratio is greater than unity, that for haddock, inhabiting a very different part of the area, is rather less than unity. The changes in the concentration imply that the simple ratio of total catch to total effort may change by 13 % for plaice, and 41 % for haddock purely because of changes in the distribution of the fishing, without any real change in density.

Ideally, the choice of sub-areas should be such that (i) they cover the whole stock of fish, (ii) the distribution of fish and fishing is regular within each, and (iii) some fishing is done in each, so as to provide an index of density. Often the fishing activities of a single country do not cover the whole stock. For instance, the English trawl fishery extends only erratically east of 4° E., so that English statistics alone cannot give a fully accurate index of the whole North Sea plaice stock; nor does the limit of consistent English trawling appear to correspond with any limit of a real biological subdivision of the plaice stock. However, the fishing by all countries taken together does cover pretty well the whole North Sea. Therefore, provided the units of effort of each country are properly calibrated (see BEVERTON and PARRISH, 1955), an accurate index of density for the whole North Sea stock could be obtained by detailed combined international statistics.

A final source of variation in the relation between catch per unit effort and density lies in possible variation in time. This corresponds almost exactly with the effects of changes in distribution in space and may be corrected in the same way. In many fisheries particularly for pelagic species the catch per unit effort changes, due to changes in behaviour of the fish, e. g., spawning concentrations, from season to season within the year. In general, more fishing will be done at times when the catch per unit effort is high, and if in one year proportionally more fishing is done at this time, the total catch will increase, giving an apparent increase in density. Just as for uneven spatial distribution, the year may be divided into periods, within each of which the catch per unit is more nearly constant. Then, the annual index of density, relatively free from changes in the temporal distribution of fishing, will be given by the mean of the catch per unit effort within each period.

All these corrections may be combined together to give the best index of density for the year. Within each interval of time and sub-area, the density index is the catch per standard unit of effort, and the density index for the year over the whole region, will be the mean of these separate catches-per-unit-effort. The ratio of this index to the average density will be effectively constant. The area covered by the stock generally remains constant from year to year, so the index of density will serve equally well as an index of abundance, or of total numbers. If the area is variable then the index of abundance will be area × index of density.

In estimating the structure of the population, that is its relative size and age composition, bias is a far bigger problem than variance. Even a small number of hauls on the same spot will give a very consistent composition of the catch, though this may well not be the true composition of the population at that spot. Thus the variance over the very large number of hauls in a commercial fleet's activities will be very small. Bias may be considered in two parts; first, the structure of the population at the fishing position may not be typical of that of the whole population; secondly, the structure of the catch may not be the same as that of the population at the position of capture. The first of these has the same effect as the uneven distribution of fishing and density of fish, and may be dealt with in a similar way. For instance, in the North Sea plaice fishing, if more ships fished off the continental coast, i. e., on grounds typically containing small plaice, instead of on the Dogger Bank —typically containing large plaice,—then relatively more small plaice would be landed, and the apparent structure of the population would be altered. By dividing the area into sub-areas, and treating the density of each age or length group separately, in the same way as in obtaining a correct density index for the whole population, a correct structure for the whole population may be obtained. This method involves not only estimates of structure, but also of abundance, but this is unavoidable if the structure of the whole population, i. e., the relative abundance of different groups, is to be estimated when they are separated into partly different areas. If no estimates of density can be made, some idea of the structure of the population, particularly of its change, can still be obtained which will not be disturbed by changes in the distribution of the fleet. Suppose the whole region is divided up into areas in each of which the structure is uniform, and hence may be estimated at once from the catches, then the true structure will be the weighted mean of the structures in each area, the weighting factors being the abundance in each area. This will not be known, but if some other constant weighting factors are taken, then the resulting estimate for the structure will be unaltered by changes in the distribution of the fishing between the various areas. It will not be the true structure, but will be reasonably close, and in particular will quite well reflect changes in the population structure.

The landings of fish from a particular area will differ in structure from the true population in that area. This may be due to rejection of small fish, selection of small fish through the meshes of the net, or differential capture of large and small fish other than by mesh selection. The first two are only important over a limited and usually easily determined size range, but the third is much more difficult to determine. It will be noticeable when two or more gears operating on the same part of a stock have catches with different structures, e. g., the long-line, gill-net and purse-seine catches of cod at Lofoten (Rollefsen, 1953). Then escapement must be taking place for at least two of these gears—probably long-line and gill-nets. Though this means that the long-line and gill-net catches are no use for direct estimation of the population, it also means that the effect of the gear on the population cannot be represented by the same mortality coefficient for all age-groups. If the non-representative gear takes a fair proportion of the total catch, so that its effect on the population is important, then the catches from it will have to be sampled, to give the catches and hence the mortalities in each age-group separately. This problem is discussed further by Margetts (1955).

The above review is not an exhaustive survey of all sources of bias and variance arising in sampling fish populations; also, particularly in estimating the population from the catch, several likely sources of error have been mentioned, but assumed to be small in default of methods of correcting for them. Some comfort, however, that the major sources of variation have been accounted for in one fishery may be gained from an analysis of the Lowestoft plaice sampling. For the three biological years April 1950—March 1953, the expected variance in the estimated numbers of each year-class were calculated. From these the expected variance in the exponential mortality rates was calculated, and was 0·034. At the same time the actual observed variance for the set of 12 separate estimates of mortality, for the 6 most abundant and fully recruited year-classes for the two pairs of years 1950—51 and 1951—52 was calculated, and was 0·027. The reasonably close agreement between the two is a fair indication that the known and calculable sources of variance are the most important. That is, the sampling of a fish population by a commercial fleet can in some circumstances at least probably give estimates within a predictable and not too large margin of error.

## 3.

# A Note on the Statistical Distribution of Trawl Catches.

*By* J. A. Gulland

In considering experiments involving series of trawl hauls, particularly if the number is small, some account has to be taken of the statistical distribution of the catches. Proper statistical treatment will enable not only the best use to be made of the available data after the experiment, but should enable the experiment to be planned in the most efficient manner.

The observed distribution of catches may be considered in two parts; first, the distribution of catches at, as far as possible, the same place and time, and secondly, the distribution of catches from different positions. If the distribution of fish was random, both these distributions would be Poisson. However, it is well known that some places are more favoured by fish than others, so that the form of the second distribution would be expected to contain a few high values, corresponding to hauls in the favoured localities, and more low values, corresponding to hauls in unfavourable positions. The exact form of the distribution will, of course, depend largely on the positions of the hauls; for instance, the number of zero catches can be arbitrarily increased by taking extra hauls in completely unfavourable positions. The fitting of exact mathematical distributions is therefore meaningless, though the general form of the distribution will usually be something like one of the so-called contagious distributions, and may in any given case be well fitted by one or more of these.

Turning to the first type of distribution, we will consider hauls at each different position as being samples from different statistical distributions. The particular distribution will be determined in general mainly by the species of fish, their density, and the type, and particularly fishing power of the gear used. Of particular interest will be the mean number caught ($m$) and the variance ($s^2$), and the relation between them. If the fish are distributed randomly, i. e., the probability of a fish being in the sample is not altered by the fact that another is present, then the distribution will be Poisson, and in particular the variance will be equal to the mean, that is

$$s^2 = m. \qquad (1)$$

From direct observation it is known that many species of fish tend to shoal together, so that they are not randomly distributed, i. e., the presence of one fish increases the probability of another being present. Thus the distribution will not be Poisson but some sort of contagious distribution, and the variance will be somewhat greater than the mean, and the relation between them may be written in the form

$$s^2 = am + bm^2. \qquad (2)$$

The observed distribution of catches of repeated hauls is also likely to depart from Poisson because of changes in the efficiency of the gear, and in the population sampled. The first of these has been suggested as a reason for the non-Poisson distribution of plankton hauls by Winsor and Clarke (1940). The difficulty of ensuring that the population sampled remains constant is, for plankton populations, demonstrated in the paper by Barnes and Marshall (1951). Here by using pumps, the variations in the efficiency of the gear was reduced to a minimum, but even in the short space covered in each series of experiments several highly significant changes in population were observed. Even in the parts where no *significant* changes in population occurred it is quite possible that small, but not probably significant, changes did take place, and that these changes accounted for the observed departures from Poisson distributions.

Such changes in efficiency, or in the populations sampled, particularly the former, might be expected to give rise to a constant coefficient of variation, i. e., standard deviation proportional to the mean, or variance proportional to the square of the mean. Adding this to the variance inherent in the Poisson distribution we have

$$s^2 = m + bm^2. \qquad (3)$$

It is worth noting that when $m$ is small, $bm^2$ will be small, so that the variance will be nearly equal to the mean, i. e., the distribution agrees well with Poisson, the discrepancy increasing with $m$. Equation (3) is of course very similar to equation (2), and the latter will be taken as typically representing the variance of repeated hauls.

From equation (2) it follows that the distribution of catches with, say, two separate gears, or at different places will differ both in mean, and in variance. This difference in variance is a definite disadvantage in

statistical analysis, making such powerful methods as the analysis of variance inapplicable. It can be overcome by using some suitable function, e. g., the logarithm, of the actual catch as the observed value for the purposes of analysis. If the constants $a$ and $b$ were known, the transformation which would result in all distributions having the same variance could be determined. In default of a knowledge of $a$ and $b$ it is only possible to find a transformation which serves to make the observed variances substantially the same. Such a transformation is the logarithm of the catches (or the catches $+1$ to avoid trouble with zeros), as for instance has been used by PARRISH (1951). Its effect may be illustrated by the table below, based on PARRISH's data.

**Table 1. The mean Catch (in Numbers) of Plaice by four different Gears, with the Variance of the Numbers, and the Variance of their Logarithms.**

| Ship and gear | Mean catch | Variance (nos.) | Variance (logs.) |
|---|---|---|---|
| "Explorer", with tickler ..... | 171·5 | 4324·0 | 0·032 |
| "Explorer", without tickler ... | 7·8 | 33·8 | 0·117 |
| "Sir Lancelot", with tickler.... | 203·5 | 3713·4 | 0·019 |
| "Sir Lancelot", without tickler. | 63·7 | 538·2 | 0·021 |

This gives the variances of the original, and the transformed, data, showing how the variance of the transformed data has been made much more nearly constant. Though there is possibly a suggestion that now the variance actually decreases with the mean, this effect may well be due to a chance sampling effect, the variances being only based on some eighteen observations. Certainly there is not sufficient evidence to abandon the log transformation for something more complicated; and it would seem, in default of intensive investigation of the problem, that this transformation is suitable for most statistical analyses of trawl data.

The form of equation (3) has further implications in the design of investigations; for example, a trawl survey for estimating the abundance of a stock of fish. In any large and heterogeneous area, such a survey is best conducted by stratified sampling, i. e., dividing the area up into sub-areas in each of which the density of fish is comparatively uniform, in a similar manner as is suggested for the analysis of commercial statistics (see BEVERTON and PARRISH, No. 8, and GULLAND, No. 2). To sample most efficiently, i. e., with the least variance for a given effort, the amount of sampling, i. e., number of hauls, should be proportional to the standard deviation in that sub-area (see DEMING, 1950). This is given by equation (2), which therefore determines the sampling pattern; for example, if one area has twice the density of fish, it will require about twice as many hauls. It may also be used to determine the size of the individual sample, e. g., whether to make a few long hauls with a powerful gear, or to make shorter hauls with a smaller gear. For this, we may now consider the $m$ of equation (2) to be determined, not by the density of fish, but by the fishing effort of the sampling gear. It will be assumed that the variance of the catches of a powerful gear used for a short time, and of a small gear towed for a long time, will be the same if their mean catch is the same. We are now interested, not so much in the variance of the catch, but the variance of the estimate of the population abundance. In this discussion we may assume that the raising factor needed to estimate total abundance from the average catch is known. It will be inversely proportional to $m$, equal to $c/m$, say. Then, if, say, $n$ hauls are made, with catches $m_1, m_2 \ldots\ldots m_n$, then the estimate of total abundance $N$ is

$$N = 1/n\,(m_1 + m_2 + \cdots\cdots m_n) \times c/m$$

and variance $N = 1/n \times$ variance $m \times (c/m)^2$

$$\therefore \text{ variance } N = \frac{c^2}{n}\left(\frac{a}{m} + b\right). \qquad (4)$$

In equation (4) the two factors which may be varied are $n$ and $m$; increasing either of them will reduce the variance. However, they are not quite independent; for instance, making longer tows will decrease the possible number of hauls in a given time. In general, though, the number of hauls will be independent of the type of gear, so that increasing the fishing power (see BEVERTON and PARRISH, No. 8), of the sampling gear is bound to decrease the variance. The best length of haul will depend on the relative values of $a/m$ and $b$, and also on the distance between stations. To take the extreme case, if this latter is negligible, so that we can assume that all the available time is spent fishing, then $nm$ is proportional to $T$, the available time, and we have

$$\text{Variance } N = c^2\left(\frac{ak}{T} + \frac{b}{n}\right) \text{ where } k = \text{constant.}$$

This would appear to be the condition implicitly assumed by TAYLOR (1953). From this it follows that for minimum variance $n$ is made as large as possible, i. e., that $m$ is as small as possible, and the hauls are very short. For large steaming time between stations, the increased number of stations attained by reducing the average length of haul will not be so great, so that the best length of haul will be greater. From this discussion it follows that the best sampling gear is normally the most powerful available, used in reasonably short hauls, subject always to the points brought out by MARGETTS (No. 5) that throughout any sampling programme the sampling gear should be kept exactly constant, and all its details recorded.

## 4.

# The Analysis of Trawl Haul Statistics with Particular Reference to the Estimation of Survival Rates.

*By* R. Jones

### Introduction.

The analysis of the results of experimental trawling surveys can take many forms and to describe all in detail would clearly require far more space than can be devoted here. One analytical technique that is of particular interest and value, however, is that of transforming data to logarithms. It is the object of this part of the paper to show how useful this may be, particularly in the determination of survival rates.

If a large number of trawl hauls of the same duration are made on any fishing ground, the frequency distribution of numbers of fish caught is usually highly skewed. Some results from research ship sampling are shown in Figures 1 and 2, and the phenomenon is often observed in samples from commercial landings also. Such data do not immediately lend themselves to statistical analysis. For one thing, if the data are not normally distributed, the arithmetic mean of the observations may not necessarily be the most efficient estimate of the population mean. Also, a comparison of two means using "Students t-test" requires that the variance of the individual observations be independent of their means. In these particular skew distributions, this condition is not satisfied, the variance being related to the mean. Two of the main objects of transforming data (Bartlett, 1947) are to correct for this dependence and to normalize the distribution of the variate.

A number of transformations have been derived for these reasons. These include:—

(a) The square-root transformation. This is used when it is found that the mean and variance are proportionately related.
(b) The inverse sine transformation. This is used for comparing percentages.
(c) The logarithmic transformation. This is used when the mean and standard deviation are proportionately related.

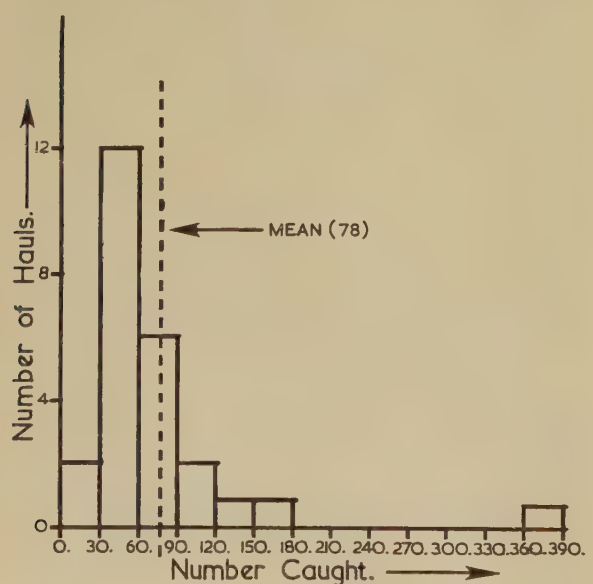



Figure 1. Frequency histogram of the numbers of haddock taken by F. R. S. "Explorer". Area C13c, May 1952. 25 one-hour hauls, without sweeps.

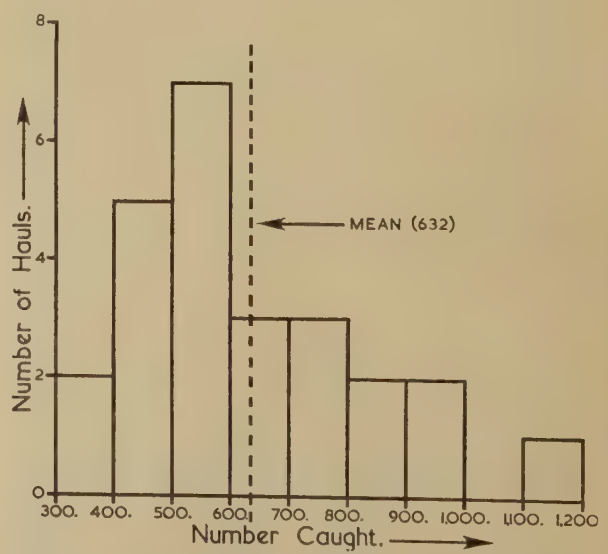



Figure 2. Frequency histogram of the numbers of haddock taken by F.R.S. "Explorer". Area C13c, May 1952. 25 one-hour hauls, with sweeps.

This has generally been found to be true of the numbers of fish taken in successive trawl hauls on any ground (Barnes and Bagenal, 1951; Taylor, 1953), and for this reason, the logarithmic transformation has been chosen for the analysis of trawl haul data.

The application of the logarithmic transformation to the determination of survival rates necessarily involves a certain amount of statistical theory, and this has been presented in detail in a later section. In the section below, theoretical consideration will be kept to a minimum and as far as possible the methods will be illustrated by means of examples.

The survival rate of a year-class of fish is generally determined from the ratio of its numbers when sampled at annual intervals. Such numbers are usually expressed as "numbers of fish per unit fishing effort" and the assumption is made that this measure is a true index of the population density at the time. If only one such pair of numbers is available, an estimate ($\overline{P}$) of ($P$) the survival rate is given by:

$$\overline{P} = \frac{y_2}{y_1}$$

where $y_1$ and $y_2$ are the catches per unit effort of a given brood sampled at two intervals of time.

Suppose now that several independent estimates of survival rate are available

$$\text{i. e. } \frac{y_{2\cdot1}}{y_{1\cdot1}} = \overline{P}_1$$

$$\frac{y_{2\cdot2}}{y_{1\cdot2}} = \overline{P}_2$$

$$\frac{y_{2\cdot3}}{y_{1\cdot3}} = \overline{P}_3 \text{ and so on.}$$

There are three ways in which these estimates of survival rate may be combined to give an overall mean estimate.

(a) The three estimates $\overline{P}_1$, $\overline{P}_2$ and $\overline{P}_3$ can be simply averaged. This will be appropriate if the quantities $\overline{P}$ are normally distributed about the true mean ($P$), in which case their mean value can be expected to be both unbiased and the most efficient possible from the data. The tendency for the $y$'s to be lognormally distributed, however, has already been mentioned (i. e., the logarithms of the $y$'s tend to be normally distributed). It follows then from the arguments set out in the next section that the mean of the $P$'s gives a biased and inefficient estimate of the true survival rate $P$.

(b) A second method is to sum all the $y_1$'s and all the $y_2$'s and determine the ratio of their totals:

$$\text{i. e. } \overline{P} = \frac{y_{2\cdot1} + y_{2\cdot2} + y_{2\cdot3}}{y_{1\cdot1} + y_{1\cdot2} + y_{1\cdot3}}.$$

If this is done, more weight is given to large numbers than to small ones. Large numbers, however, tend to have a greater error variance than small ones, so that weighting in this manner will not give the most efficient result either.

(c) In (a) reference was made to the fact that the quantities $y$ tend to be lognormally distributed. This is also true of the $\overline{P}$'s and the possibility therefore suggests itself of taking their logarithms, averaging these and then antiloging the result.

$$\text{i. e. } \overline{P} = 10^{(\log P_1 + \log P_2 + \log P_3)/3}.$$

This in fact is the geometric mean of the $P$'s and, although an efficient estimate, it is not unbiased. To allow for this it is necessary to include a correction factor before antiloging as will be apparent from the following examples.

## Determination of Survival Rates.

### Section I. General Considerations.

**The estimation of a survival rate as a ratio.**

It will be assumed that on two occasions, a year apart, a series of hauls have been made and the catches per unit effort have been determined in each case. Then, following the reasoning given in (c) above, it is shown later that an approximately unbiased estimate of survival rate is given by

$$\overline{P} = 10^{-(\bar{x}_1 - \bar{x}_2) - 1.1515 s^2/N}$$

where $\bar{x}_1$ and $\bar{x}_2$ are the means of the logarithms[1]) of the catches per unit effort on the first and second occasions respectively, $s^2$ is the pooled "within group" variance of the two "$x$" series, and $N = \frac{n_1 \cdot n_2}{n_1 + n_2}$ where $n_1$ and $n_2$ are the number of hauls made on each occasion. Confidence limits may be determined from the expression

$$\overline{P} \cdot 10^{\pm ts/\sqrt{N}}$$

where $t$ is "Student's" $t$ and can be looked up in statistical tables for the level of probability required.

[1]) In this section of the text, it is assumed that logarithms to the base 10 are used. For theoretical purposes however, it is more convenient to use logarithms to the base $e$, and this has been done in a later section.

**An extension of the simple method.**

Let us suppose that instead of two series of hauls each made one year apart we have two series each spread out over a number of months. It will be supposed that these can be arranged in pairs, so that for every month in the first series (the $x_1$ series), there is a comparable estimate for a similar month in the second series one year later (the $x_2$ series). In that case like months can be paired off and from each pair an estimate of survival rate obtained. The problem then is to combine these estimates in the most efficient manner. The method of doing this is fundamentally the same as that stated above and an approximately unbiased estimate of survival rate is given by

$$\overline{P} = 10^{-(\bar{x}_1 - \bar{x}_2) - 1.151\, s^2/M}$$

from (equation (14) in section II)

where $\bar{x}_1$ and $\bar{x}_2$ are the means of the logarithms of the present two series of numbers, $M$ is the number of pairs of observations and $s^2$ is the variance of the differences between the logarithms of the catches per unit effort in like months (i. e., the variance of the quantities $x_1 - x_2$). It should be noted therefore that $s^2$ in this case is different from that in the example above.)

It is important to realize the distinction between $x_1$ and $x_2$ in this example and $x_1$ and $x_2$ in the last one. In this instance it might happen that sampling has taken place in every month for a period of two years. Then the results of the first year's sampling constitute twelve values of $x_1$ and those from the second year twelve values of $x_2$. Furthermore, if values of $x_1$ and $x_2$ from like months are paired off a single series of twelve values $(x_1 - x_2)$ will be obtained. $s^2$ will then be the variance of these twelve values. In the previous example, on the other hand, it was supposed that $n_1$ values of $x_1$ were obtained more or less simultaneously and that the $n_2$ values of $x_2$ were also obtained simultaneously but exactly twelve months later. In that case $s^2$ was estimated from the variances within each group separately.

An example is afforded by data collected each month on Aberdeen fish market during 1950—1953, and summarized in *Annales Biologiques* (1951—1953). This gives estimates of the catches of each group of haddock per 100 hours fishing each month by Aberdeen trawlers fishing at Faroe.

The 1950 and 1951 data were treated first, and the logarithms of the numbers caught per unit fishing effort were determined. For each brood, the logarithms of the 1950 and 1951 catches become the series "$x_1$" and "$x_2$" respectively. Like months can be paired off and each value of $x_2$ subtracted from the comparable $x_1$. These results are shown in Table 1.

In the case of the 1951—1952 estimates, the 1951 figures become the $x_1$ series and 1952 the $x_2$ series, and similarly for the period 1952—1953.

Any one of these estimates $(x_1 - x_2)$ can of course be used to give an estimate of survival rate $(P)$ from the relationship

$$\overline{P} = 10^{-(x_1 - x_2)}.$$

A mean estimate for each brood is, however, more reliable, provided there is no significant trend in survival rate during each period. In order to test this possibility, a regression of the values $(x_1 - x_2)$ on the months (1, 2, 3 etc.) was carried out, and these regression coefficients are included in Table 1. Neither singly nor collectively were these found to be significant so that mean estimates were obtained.

The next step was to test whether the different mean values of $(x_1 - x_2)$ for each brood differed significantly from one another. This was tested by an analysis of variance for each period separately. The analysis for the 1950—1951 period is given in Table 2.

**Table 2. Analysis of 1950—1951 Data.**

| Source of variation | Degrees of freedom | Sums of squares | Mean sq. | F. |
|---|---|---|---|---|
| Total ..... | 42 | 3·5488 | — | — |
| Within Broods... | 38 | 2·9053 | 0·07645 | — |
| Between Broods . | 4 | 0·6435 | 0·1609 | 2·10 |

Comparable analyses for the periods 1951—1952, and 1952—1953, gave $F$ values of 1·22 and 1·96 respectively, which, like the 1950—1951 value, were not significant. The mean values of $(x_1 - x_2)$ for each of the periods (1950—1951, 1951—1952 and 1952—1953) were then computed for all broods and found to be 0·5658, 0·3183 and 0·2768 respectively. The pooled "within brood" variances ($s^2$) for each period were 0·07645, 0·07588 and 0·1049 respectively. There was no significant difference between these estimates of variance and all were pooled to give a mean $s^2$ equal to 0·08944.

**Table 1. Differences $(x_1 - x_2)$ between the Logarithms of the Catches per 100 Hours Fishing of Faroe Haddock Broods in the same Months in 1950—1951.**

| Brood | Jan. | Mar./Apr. | June | July | Aug. | Sept. | Oct. | Nov. | Dec. | Regression coefficient |
|---|---|---|---|---|---|---|---|---|---|---|
| 1948 ..... | — | — | 0·9217 | 0·2653 | 0·6114 | 0·4625 | 0·8221 | 0·6053 | 0·6949 | 0·00751 |
| 1947 ..... | 0·7930 | 0·1695 | 0·7208 | 0·4905 | 0·6122 | 0·4996 | 0·8101 | 0·5610 | 0·7704 | 0·02120 |
| 1946 ..... | 0·5874 | 0·4465 | 0·5324 | 0·9152 | 1·0079 | 0·7177 | 1·3717 | 1·1399 | —0·1230 | 0·01203 |
| 1945 ..... | 0·8911 | 0·4358 | 0·5712 | 0·3641 | 0·5292 | 0·1744 | 0·6389 | 0·5818 | 0·3368 | —0·03056 |
| 1944 ..... | 0·1447 | 0·2631 | 0·5565 | 0·1121 | 0·3177 | 0·4047 | 0·4920 | 0·8145 | 0·2953 | 0·04054 |

A comparison of the three mean values of $(x_1 - x_2)$ above showed that the 1950—1951 value (0·5658) differed significantly from the other two, which were not significantly different from one another. A pooled estimate for the periods 1951—1952, and 1952—1953 was therefore made, giving a value of 0·2925.

Finally, final estimates of the survival rates ($\overline{P}$) were obtained.

Period 1950—1951

$$\overline{P} = 10^{-(0.5658) - \frac{0.08944}{43}(1.151)}$$
$$= 0{\cdot}270 \text{ i. e., } 27\,\% \text{ annually.}$$

Periods 1951—1952 and 1952—1953

$$\overline{P} = 10^{-(0.2925) \quad \frac{0.08944}{116}(1.151)}$$
$$= 0.509 \text{ i. e., } 51\,\% \text{ annually.}$$

The 95 % confidence limits for these are: (from equation (15) in section II):

Period 1950—1951

$$(0.270)\, 10^{\pm (1.975)\left(\frac{0.08944}{43}\right)^{1/2}}$$
$$= 0.219 \text{ and } 0.332 \text{ i. e., } 22\,\% \text{ and } 33\,\% \text{ annually.}$$

Periods 1951—1952 and 1952—1953

$$(0.509)\, 10^{\pm (1.975)\left(\frac{0.08944}{116}\right)^{1/2}}$$
$$= 0.449 \text{ and } 0.577 \text{ i. e., } 45\,\% \text{ and } 58\,\% \text{ annually.}$$

From these results it appears that there was a significant increase in the survival rate of Faroe haddock after 1951.

In the previous example, estimates of density (from catches per unit effort) were made each month over a period of years, so that it was possible to pair off like months to give a series of estimates of survival rate. Suppose, now, that sampling had been less regular, so that such a pairing off was impossible. This case is considered in section II where the additional assumption has been made that catches per unit effort in different months give comparable measures of density. The procedure here is simply to take logarithms of the catches per hours fishing of each brood and to calculate the regression of these on age at time of capture (Parrish and Main, 1950).

For example, let us consider the average catches per unit fishing time of North Sea haddock by F.R.S. "Explorer" over a period of several years. The data, in the form of average annual catch per 10 hours fishing of each brood, from several areas of the North Sea, are available in *Annales Biologiques* (1951—1953). As a particular example, the 1947 and 1948 broods have been analysed, and the logarithms of the numbers caught per 10 hours fishing are shown in Table 3.

**Table 3. Logarithms of the Numbers of different Haddock Broods from different Areas in the North Sea with Regression Estimate ($\bar{r}$) and survival Estimate ($\overline{P}$).**

| Age (yrs.) / Area / Brood | Northern Area 1947 | Northern Area 1948 | North Central Area 1947 | North Central Area 1948 | Central Area 1947 | Central Area 1948 |
|---|---|---|---|---|---|---|
| 2 | 2·5038 | 2·5899 | 1·8976 | 2·6785 | 1·8808 | 2·5563 |
| 3 | 2·0607 | 2·5478 | 1·3222 | 1·9868 | 1·0792 | 1·4771 |
| 4 | 1·6721 | 1·8325 | 0·6021 | 1·5441 | 0·3010 | 1·1139 |
| 5 | 0·9031 | 1·3426 | 0·3010 | 0·3010 | 0·0000 | 0·7782 |
| 6 | 1·0000 | — | — | — | — | — |
| $(\bar{r})$ | –0·4165 | –0·4458 | –0·5510 | –0·7575 | –0·6421 | –0·5697 |
| var $(\bar{r})$ | 0·0049 | 0·0097 | 0·0097 | 0·0097 | 0·0097 | 0·0097 |
| $\overline{P}$ | 0·378 | 0·349 | 0·274 | 0·174 | 0·222 | 0·262 |
| 95 % limit of $\overline{P}$ | ·27–·54 | ·21–·57 | ·17–·45 | ·11–·28 | ·14–·36 | ·16–·43 |

$\bar{r}$ is the slope of the regression of log number on age. $\overline{P}$ is an estimate of survival rate determined by the following expressions (see equation (21), section II).

$$\overline{P} = 10^{\bar{r} - 1.151 \text{ (var } \bar{r})}$$

with 95 % confidence limits

$$\overline{P} \cdot 10^{\pm t\, (\text{var } \bar{r})^{1/2}}$$

Using these expressions, estimates of $\overline{P}$ along with their 95 % confidence limits were determined, and are shown in the last two rows of Table 3. Estimates of the variance of $\bar{r}$ were made from a pooled estimate of residual variance equal to 0·0487. The differences between these values of $\overline{P}$ are non-significant, and so a pooled estimate of 0·29 was determined with 95 % limits of 0·24 and 0·34.

A last example of the estimation of survival rates deals with the analysis of the returns of plaice tagged on the east coast of Scotland. These results have been dealt with in three groups:— (a) data taken from Fulton (1920), (b) experiments carried out between 1920 and 1939, and (c) data collected after the second World War. The data in (b) and (c) were kindly placed at my disposal by my colleague Mr. E. Wilson. They are summarized in Table 4.

The determination of annual survival rates in this case was carried out as in the previous section, by fitting a linear regression of the logarithms of the numbers returned on period of recapture.

Estimates of survival rate ($\overline{P}$) were obtained, as before, from the expression

$$\overline{P} = 10^{\bar{r} - 1.151 \text{ var } (\bar{r}}$$

with confidence limits

$$\overline{P} \cdot 10^{\pm t\, (\text{var } \bar{r})^{1/2}}$$

$\bar{r}$ is the slope of the regression. These results are given in Table 4.

**Table 4. Returns of marked Plaice and Estimates of survival Rate.**

| Data from FULTON (1920) (by 3 monthly periods) | | 1920–39 data (by yearly periods) | | Post-war data (by 6 monthly periods) | |
|---|---|---|---|---|---|
| Return periods ($t$) | No. returned | Return periods ($t$) | No. returned | Return periods ($t$) | No. returned |
| 0 | 952 | 0 | 1446 | 0 | 441 |
| 0·25 | 790 | 1 | 165 | 0·50 | 65 |
| 0·50 | 537 | 2 | 6 | 1·00 | 38 |
| 0·75 | 484 | 3 | 1 | 1·50 | 7 |
| 1·00 | 290 | .. | .. | .. | .. |
| 1·25 | 194 | .. | .. | .. | .. |
| 1·50 | 146 | .. | .. | .. | .. |
| 1·75 | 102 | .. | .. | .. | .. |
| 2·00 | 68 | .. | .. | .. | .. |
| 2·25 | 60 | .. | .. | .. | .. |
| 2·50 | 29 | .. | .. | .. | .. |
| 2·75 | 21 | .. | .. | .. | .. |
| Number liberated ($N_0$) | 7166 | 3834 | | 996 | |
| Slope of regression ($\bar{r}$) | –0·6090 | –1·092 | | –1·1262 | |
| ($Z$) | 1·402 | 2·515 | | 2·594 | |
| Estimate of survival $\overline{P}$ | 0·246 | 0·079 | | 0·070 | |
| 95 % limits of $\overline{P}$ | 0·223–0·271 | 0·034–0·185 | | 0·015–0·337 | |
| intercept $\bar{a}$ | 3·0552 | 3·1770 | | 2·5650 | |
| $\overline{F}$ | ·75 | 1·07 | | 1·32 | |
| $\overline{M}$ | ·65 | 1·44 | | 1·27 | |

The next step in this calculation was to obtain an estimate of the mortality rates due to fishing ($F$) and other causes ($M$) respectively. These are shown to be jointly related to ($P$), the annual survival rate, by:—

$$P = e^{-(F+M)} \text{ or } P = e^{-Z}$$

where $Z = F + M$.

It follows then, from the arguments in the next section, that an estimate of $Z$ is given directly from the slope of the regression line ($\bar{r}$)

$$\text{i. e. } \overline{Z} = -2{\cdot}303\bar{r}.$$

An approximate estimate of $F$ is derived in section II and given by

$$F = \frac{\overline{Z}\,10^{\bar{a}}}{N_0(1-10^{\bar{r}q})}$$

where $N_0$ is the number of fish liberated.

$\bar{a}$ is the intercept of the regression line on the "log number" axis and $q$ is the fraction of a year covered by each period of recapture.

Finally, an estimate of $M$ was obtained in each instance from:—

$$\overline{M} = \overline{Z} - \overline{F}.$$

Before any interpretation can be put on these results, it is important that the exact significance of the parameters $\overline{Z}$, $\overline{F}$, and $\overline{M}$ is understood.

(a) $\overline{Z}$ is the total mortality rate from all causes, operating at each successive instant of time. It is made up of mortality due to fishing, to natural causes and to the effect of tagging, as well as necessarily including a component representing emigration from the tagging area.

(b) $\overline{F}$. The calculation of this, the fishing mortality rate, involves the extrapolation of numbers of recaptures back to the time of liberation. In this way an estimate is obtained of the rate of capture at that moment, in terms of a known number of fish liberated. There are two unknown factors that might influence this estimate.

(i) Any tagging mortality at the time of liberation will reduce the number of live, tagged fish in the sea by an unknown amount. Since $\overline{F}$ will then be estimated from the number liberated instead of the number of survivors it will tend to be underestimated.

(ii) The calculation of $\overline{F}$ also presupposes that all tagged fish that are caught are actually recorded. Therefore any tendency for fishermen to fail to hand over tagged fish will also result in an underestimate of fishing mortality.

Since both these possibilities are bound to occur, any estimate of fishing mortality by this method is almost certain to be underestimated to some extent.

(c) $\overline{M}$. This estimate includes natural mortality, tagging mortality after the time of liberation, and emigration from the tagging area. For these reasons alone, as an estimate of natural mortality proper, $\overline{M}$ is almost certain to be overestimated. Also, since $M$ is estimated by subtracting $\overline{F}$ from $\overline{Z}$ any tendency for $\overline{F}$ to be underestimated will further tend to overestimate $\overline{M}$.

These effects will inevitably make $\overline{M}$ large as is evident from the values of $\overline{M}$ given in Table 4.

## Section II. Theoretical Aspects.

In an earlier section it was pointed out that the numbers of fish taken in successive trawl hauls tend to follow a skew distribution but that the logarithms of these numbers are approximately normally distributed. A particular application of this property of the data arises in the determination of survival rates and will be outlined below.

Let the annual survival rate ($P$) be defined as

$$P = \frac{N_2}{N_1} \tag{1}$$

where $N_1$ is the absolute density of an age group of some species at any time and $N_2$ is its density twelve months later.

Now, if it is assumed that catches per unit effort by trawling at these two times give comparable measures of the absolute densities $N_1$ and $N_2$, it is possible to write:—

$$P = \frac{\mu_2}{\mu_1} \tag{2}$$

where $\mu_1$ and $\mu_2$ are the expected catches per unit effort comparable with $N_1$ and $N_2$ respectively.

$\mu_1$ and $\mu_2$ are of course unknown. Instead a series of observations $y_1$ and $y_2$ will be available from successive trawl hauls and, as a first approximation, an estimate ($\bar{P}$) of $P$ might be given from the ratio of the means of the two sets of observations, i. e.,

$$\bar{P} \quad \frac{\bar{y}_2}{\bar{y}_1} \tag{3}$$

where $\bar{y}_1$ and $\bar{y}_2$ are the mean numbers caught per unit effort at annual intervals. Such an estimate is not necessarily either the most efficient, or even an unbiased one, and a means of satisfying both these requirements will be considered below. In order to determine whether the estimate of $P$ given by (3) is unbiased, it is necessary to consider whether the expectation of $\bar{P}$ is equal to $P$. Before attempting this, it is convenient to consider the expectations of the numerator and denominator separately. A short digression is relevant here to consider the relationship between the mean of a set of observations and the mean of their logarithms. This will be made before continuing with the main theme.

### The relationship between the mean of a set of observations and the mean of their logarithms.

Let us suppose that we have a series of $n$ observations

$y_1, y_2, y_3 \cdots\cdots y_n$ and their corresponding logarithms $x_i$,

$x_1, x_2, x_3 \cdots\cdots x_n$.

Each $x_i$ will be defined so that

$$x_i = \log_{10}(a + y_i) = 0.4343 \log_e (a + y_i) \tag{4}$$

where $a$ is an arbitrary constant, often made equal to unity.

It will be supposed that the quantities $x_i$ are normally distributed about a true population mean $\varepsilon$ and variance $\sigma x^2$. It is required to express the mean of the $y$'s in terms of the parameters of the $x$ distribution (i. e., $\varepsilon$ and $\sigma x^2$).

From (4) we get

$$a + y_i = e^{2.303 x_i} = 10^{x_i}\ ^1).$$

The mean or expected value of $(a + y_i)$ will therefore equal the expected value of $e^{2.303 x_i}$.

This is immediately obtained from the moment generating function of the normal distribution (Weatherburn, 1949), as:—

$$\left.\begin{aligned} E\{a + y_i\} = E\{e^{2.303 x_i}\} &= e^{2.303\varepsilon + 2.652\sigma_x^2} \\ &= (a + \mu) \text{ say} \end{aligned}\right\} \tag{5}$$

where $\mu$ is the true mean of the population from which the observations $y_i$ were initially drawn.

We have then, that

$$\mu = e^{2.303\varepsilon + 2.652\sigma_x^2} - a. \tag{6}$$

In practice, (6) cannot be used for estimating ($\mu$), since neither $\varepsilon$ nor $\sigma_x{}^2$ are known. Instead there will be estimates of these parameters ($\bar{x}$ and $s^2$), determined from the mean and variance of the sample of $x$'s.

It is shown in the appendix that the substitution of $\bar{x}$ and $s^2$ for $\varepsilon$ and $\sigma_x{}^2$ in (6) would lead to a biased estimate of $\mu$, and that an approximately unbiased estimate is given by the expression:—

$$\left.\begin{aligned} \bar{\mu} &= e^{2.303\bar{x} + 2.652 s^2\left(\frac{n-1}{n}\right)} \\ &\left[1 - \frac{7(n-1)^2 s^4}{n^2(n+1)} + \frac{50(n-1)^3 s^6}{n^3(n+1)(n+3}\right] - a \end{aligned}\right\} \tag{7}$$

where $\bar{\mu}$ is an estimate of $\mu$. Further, Finney (1941) has shown that an estimate of $\mu$, determined in this manner, would be more efficient than one obtained from the straight arithmetic mean of the untransformed data, although the difference in efficiency may only amount to a few per cent.

For sufficiently large values of $n$ and small values of $s$ the terms in the large bracket in (7) above become negligible and can be ignored, and a sufficiently good approximation to $\mu$ will be given by

$$\bar{\mu} = e^{2.303\bar{x} + 2.652 s^2\left(\frac{n-1}{n}\right)} - a. \tag{8}$$

[1]) It should be noted that, although it has been more convenient to give formulae in terms of power of 10 in the text, theoretical requirements make it preferable to give them to the power of $e$ in this section.

**Setting confidence limits.**

Since it has been assumed that the distribution of the logarithms is normal, confidence limits may be set to any mean $\bar{x}$ in the usual manner. For example, if $\bar{x}$ is a mean logarithm based on $n$ observations, the true population mean ($\varepsilon$) may be expected to lie within the limits:—

$$x \pm ts/\sqrt{n} \text{ with the required probability.}$$

Therefore it will be approximately true to say that the population mean of the $y$'s (i. e. $\mu$) lies between the limits

$$\bar{\mu}\, e^{2.303\, ts/\sqrt{n}} \text{ and } \bar{\mu}\, e^{-2.303\, ts/\sqrt{n}}$$

with smiliar probability.

**Estimating survival rates.**

The survival rate ($P$) was defined in (2) so that

$$P = \frac{\mu_2}{\mu_1}.$$

Then from (6) it is now possible to write:—

$$P = \frac{e^{2.303\,\varepsilon_2 + 2.652\,\sigma_2^2} - a}{e^{2.303\,\varepsilon_1 + 2.652\,\sigma_1^2} - a}. \tag{9}$$

Provided all hauls made are of equal duration, it seems reasonable to suppose that $\sigma_1^2 = \sigma_2^2 = \sigma^2$.

If in addition, '$a$' is taken as zero, we have:—

$$P = e^{2.303\,(\varepsilon_2 - \varepsilon_1)}. \tag{10}$$

$\varepsilon_2$ and $\varepsilon_1$ of course are unknown and, instead, only $\bar{x}_2$ and $\bar{x}_1$ are available.

Following the procedure adopted above, it is possible to show that an approximately unbiased estimate of $P$ is given by:—

$$\left.\begin{aligned} \overline{P} &= e^{2.303\,(\bar{x}_2 - \bar{x}_1) - 2.652\, s^2/N} \\ &\times \left[1 - \frac{7\, s^4}{(\gamma+2)\, N^2} - \frac{50\, s^6}{(\gamma+2)\,(\gamma+4)\, N^3}\right] \end{aligned}\right\} \tag{11}$$

where $N = \dfrac{n_1\, n_2}{n_1 + n_2}$ and $\gamma = n_1 + n_2 - 2$, the number of degrees of freedom from which $s^2$ was calculated.

As in (7) the terms of $s^4/N^2$ and higher powers of $s^2$ can be ignored, giving

$$\overline{P} = e^{2.303\,(\bar{x}_2 - \bar{x}_1) - 2.652\, s^2/N}. \tag{12}$$

Confidence limits for $\overline{P}$ are given in the usual manner by

$$\overline{P} e^{-2.303\, ts/\sqrt{N}} \text{ and } \overline{P} e^{2.303\, ts/\sqrt{N}}. \tag{13}$$

The second example given in section I is fundamentally the same as that considered above. Instead of two comparable series of hauls at two times, however, we will suppose that the first series of hauls are spread out over $M$ different months. Also let the second series be spread over $M$ similar months so that for every haul in series (1) there is a comparable haul in series (2) just twelve months later.

Then, from the differences in the logarithms of the numbers caught in comparable hauls, it is possible to obtain a series of estimates $(x_2 - x_1)$ of the quantity $\varepsilon_2 - \varepsilon_1$ so that the arguments of the preceding section are still applicable.

There is one difference, however, and that concerns the estimation of $s^2$. In this example, $s^2$ would be determined from its variance within the single series of observations $(x_2 - x_1)$ and not from the pooled variances within each separate series ($x_1$'s and $x_2$'s). $s^2$ calculated in this manner can therefore be expected to be twice the value of $s^2$ determined in the preceding section. Using this new value of $s^2$, we can write instead of (12).

$$\overline{P} = e^{2.303\,(\bar{x}_2 - \bar{x}_1) - 2.652\, s^2/M} \tag{14}$$

where $M$ is the number of pairs of months.

95 % limits to $\overline{P}$ will be given by

$$\overline{P} \cdot e^{\pm 2.303\, ts/\sqrt{M}}. \tag{15}$$

The third method of estimation is one that may have to be used when observations have not been deliberately collected in either of the ways discussed above. It is more likely in that case that comparable months cannot be matched, and that comparisons will have to be made between catches per unit effort separated by an interval not equal to twelve months.

If it is assumed that the survival rate is constant over the whole period, it is possible to relate the true numerical densities of the stock at two different times by the expression

$$N_t = N_0 P^t \tag{16}$$

where $N_0$ is the density at some arbitrary instant of time, and $N_t$ is the density $t$ years later.

Then, assuming that the catches per unit effort in different months give comparable measures of density, we can write:—

$$\mu_t = \mu_0 P^t \tag{17}$$

where $\mu_0$ and $\mu_t$ are the expected catches per unit effort at the two times.

Then, if we write

$\mu_t = e^{2.303\,\varepsilon_t + 2.652\,\sigma_t^2}$ as before, and assume a common variance for $x_0$ and $x_t$, we get

$$e^{2.303\,\varepsilon_t} = e^{2.303\,\varepsilon_0} P^t. \tag{18}$$

Takings $\log_{10}$ and rearranging gives:—

$$\varepsilon_t = \varepsilon_0 + t \log_{10} P. \tag{19}$$

$\varepsilon_t$ of course is unknown, and instead a series of estimates $x_t$ (the logarithms of the numbers caught at times $t$) are available. These by definition are normally distributed about the means $\varepsilon_t$ with a common variance ($\sigma^2$), so that an unbiased estimate of $\log_{10} P$ can be determined from a straightforward regression of the log numbers on $t$.

If the true slope of the regression line is $r$, then

$$\log_{10} P = r$$

$$\text{and } P = e^{2.303\,r} \tag{20}$$

$r$ of course, is unknown, but an unbiased estimate ($\bar{r}$) is available from the slope of the regression determined above. As before, however, a bias is introduced by simply antiloging $\bar{r}$, and instead an approximately unbiased estimate of $P$ is given by:—

$$\overline{P} = e^{2.303\,\bar{r} - 2.652\,(\mathrm{var}\,\bar{r})} \tag{21}$$

where (var $\bar{r}$) is the variance of the regression coefficient $\bar{r}$.

Similarly the confidence limits will be given approximately by

$$\overline{P}\, e^{\pm\, 2.303 t\,(\mathrm{var}\,\bar{r})^{1/2}}. \tag{22}$$

One further example that is of particular interest concerns the determination of survival (and mortality) rates from the results of marking experiments.

It will be supposed that, at some particular moment, $N_0$ marked fish are released within a fishing area, and that the total number of returns during successive periods of time are recorded. From these results estimates of mortality due to both fishing and other causes are required.

It will be supposed that the mortality due to fishing and other causes is constant throughout the experimental period, and that during any instant of time, $dt$, the rate of decrease of the number of tagged fish in the sea is given by:—

$$\frac{dN}{dt} = -N(F + M) \tag{23}$$

where $F$ and $M$ are instantaneous coefficients of fishing and natural mortality respectively. In other words, a constant proportion of the surviving tagged fish are removed at any moment, $Fdt$ due to fishing and $Mdt$ due to natural causes.

After an interval of time $t$ has elapsed since the moment of tagging, the number of survivors remaining may be determined from the solution of (23). This gives:—

$$N_t = N_0 e^{-(F+M)t}. \tag{24}$$

This expression is fundamentally the same as that in (16) so that the relationship between survival rate ($P$) and ($F + M$) is

$$P = e^{-(F+M)}. \tag{25}$$

Returning now to (24), let us consider the expected number of tagged fish ($C_t$) that will be caught during the interval between $t$ and $t + q$ years.

This will be given by:—

$$\left.\begin{aligned} C_t &= FN_0 \int_t^{t+q} e^{-(F+M)t}\,dt = \\ &\frac{FN_0 e^{-(F+M)t}\,(1 - e^{-(F+M)q})}{F+M} \end{aligned}\right\} \tag{26}$$

Taking logs of both sides we get

$$\left.\begin{aligned} \log_{10} C_t &= \log_{10} N_0 + \log_{10} F + \\ \log_{10}&\left(\frac{1 - e^{-(F+M)q}}{F+M}\right) - 0{\cdot}4343\,(F+M)t \end{aligned}\right\} \tag{27}$$

As a first approximation, an estimate of $P$ may be determined from the slope of the regression of $\log C_t$ on $t$ as in the previous section; i. e., if an estimate of $-0{\cdot}4343\,(F + M)$ is given by $\bar{r}$, the slope of the regression, we have, as in (21)

$$\overline{P} = e^{2.303\,\bar{r} - 2.652\,(\mathrm{var}\,\bar{r})} \tag{28}$$

with confidence limits as in (22).

The next step is to determine separate values for $F$ and $M$, which may be done from the intercept of the regression line on the $\log C_t$ axis, when $t = 0$.

Let this be '$a$'. Then

$$a = \log_{10} N_0 + \log_{10} F + \log_{10}\left(\frac{1 - e^{-(F+M)q}}{F+M}\right). \tag{29}$$

Rearranging terms we get

$$\log_{10} F = a - \log_{10} N_0 - \log_{10}\left(\frac{1 - e^{-(F+M)q}}{F+M}\right) \tag{30}$$

$$\text{so that } F = \frac{e^{2.303\,a}\,(F+M)}{N_0\,(1 - e^{-(F+M)q})}. \tag{31}$$

As a first approximation, it has been considered sufficient to write for $F$,

$$\overline{F} = \frac{\overline{Z}\,10^{\bar{a}}}{N_0\,(1 - 10^{\bar{r}q})} \tag{32}$$

where $\bar{a}$ is an estimate of $a$ and $\overline{Z}$ an estimate of $(F + M)$.

Finally, an estimate of $M$ is given by:—

$$\overline{M} = \overline{Z} - \overline{F}. \tag{33}$$

## Summary.

When a large number of replicate hauls are taken in the same place, the frequency distribution of numbers of fish caught is usually found to be skewed.

For this reason, straightforward statistical tests cannot be applied to the data. Instead, it is first necessary to transform to logarithms before carrying out an analysis. Since it is approximately true to regard such transformed data as being normally distributed, the mean and variance of the transformed distribution can be expected to provide both unbiased and efficient estimates. These estimates, however, will be on the transformed scale and it is easily seen that a simple conversion back to numbers (by antiloging) would lead to biased results. This source of bias can be allowed for however and the theoretical procedure for doing this is the subject of section II.

Section I is devoted to four examples illustrating the application of this theory to the determination of survival rates:—

(1) The determination of survival from two sets of trawl haul data taken at two times exactly a year apart.

(2) Determination of survival from sets of observations spread regularly over at least two years at the rate of one sample per month.

(3) Determination of survival from sets of observations spread irregularly over a period of months or years.

(4) Determination of survival from tagging and recapture experiments.


## Appendix.

The relationship between $\mu$ (the population mean) and $\varepsilon$ the mean of the logarithms of numbers sampled was defined in (6) as

$$\mu = e^{2.303\,\varepsilon + 2.652\,\sigma_x^2} - a \qquad (6)$$

where $\sigma_x^2$ is the variance of the logarithms and '$a$' is an arbitrary constant, conventially equal to unity.

In practice, $\varepsilon$ and $\sigma_x^2$ are unknown, and so an attempt to estimate $\mu$ must be made using the observed estimates of these quantities, $\bar{x}$ and $s^2$.

Let us first consider the expected value of

$$e^{2.303\,\bar{x} + 2.652\,s^2}.$$

Since the estimates $\bar{x}$ and $s^2$ are distributed independently of one another, we may write

$$E\left\{ e^{2.303\,\bar{x} + 2.652\,s^2} \right\} = E\left\{ e^{2.303\,\bar{x}} \right\} E\left\{ e^{2.652\,s^2} \right\}$$

Each of these expectations follow directly from the moment generating functions of $\bar{x}$ and $s^2$ respectively, giving

$$E\left\{ e^{2.303\,\bar{x} + 2.652\,s^2} \right\} = e^{2.303\,\varepsilon + \frac{2.652\,\sigma_x^2}{n}} \left[ 1 - \frac{5.304\,\sigma_x^2}{n-1} \right]^{-\frac{(n-1)}{2}}$$

where $n$ is the number of observations from which $\bar{x}$ and $s^2$ were calculated. Clearly the substitution of $\bar{x}$ and $s^2$ for $\varepsilon$ and $\sigma_x^2$ in (6) would lead to a biased estimate of $\mu$.

As a first approximation, we might ignore the bias arising from the use of $s^2$ instead of $x^2$, giving:—

$$E\left\{ e^{2.303\,\bar{x} + 2.652\,s^2} \right\} = e^{2.303\,\varepsilon + 2.652\,\sigma_x^2 \left(\frac{n+1}{n}\right)}.$$

Suggesting

$$e^{2.303\,\bar{x} + 2.652\,\sigma_x^2 \left(\frac{n-1}{n}\right)} \text{ as an estimate of } e^{2.303\,\varepsilon + 2.652\,\sigma_x^2}.$$

Next allowing once more for $s^2$, we try

$$E\left\{ e^{2.303\,\bar{x} + 2.652\,s^2 \left(\frac{n-1}{n}\right)} \right\}$$

which is equal to

$$e^{2.303\,\varepsilon + 2.652\,\frac{\sigma_x^2}{n}} \left\{ 1 - \frac{5.304\,\sigma_x^2}{n} \right\}^{-\frac{n-1}{2}} \qquad (6.1)$$

This may be expanded to give

$$e^{2.303\,\varepsilon + 2.652\,\frac{\sigma_x^2}{n}} \times \left\{ 1 + \frac{n-1}{2}\lambda + \frac{1}{2}\frac{(n-1)}{2}\frac{(n+1)}{2}\lambda^2 + \frac{1}{6}\frac{(n-1)(n+1)(n+3)}{8}\lambda^3 \right\} \qquad (6.2)$$

where

$$\lambda = \frac{5.304\,\sigma_x^2}{n}.$$

Now the first two terms of the large bracket in (6.2) are also those of the expansion of $e^{5.304\,\frac{\sigma_x^2}{n}\left(\frac{n-1}{2}\right)}$ so that if all terms of order $\lambda^2$ and higher were to be ignored (6·2) above could be rewritten as:—

$$e^{2.303\,\varepsilon + 2.652\,\frac{\sigma_x^2}{n}} \left[ e^{2.652\,\sigma_x^2 \left(\frac{n-1}{n}\right)} \right] = e^{2.303\,\varepsilon + 2.652\,\sigma_x^2} \qquad (6.3)$$

which is the result required.

Finally, therefore, we are led to consider

$$e^{2.303\,\bar{x}+2.652\,s^2}\left(\frac{n-1}{n}\right)\{1+bs^4+cs^6+\cdots\} \quad (6.4)$$

as an unbiased estimate of

$$e^{2.303\,\varepsilon+2.652\,\sigma_x^2}.$$

FINNEY (1941) in his solution to this problem was led to consider the expression

$$e^{x+\frac{1}{2}s^2}\left\{1-\frac{s^2(s^2+2)}{4n}+\frac{s^4(3s^4+44s^2+84)}{96n^2}\right\} \quad (6.5)$$

as an estimate of the same quantity (N. B. FINNEY used logs to the base 'e' instead of '10'). This expression, however, converges less rapidly than (6·4) as may be seen by comparing (6·5) with (6·8).

In order to determine the expectation of (6·4), it is first convenient to consider the expectation of $(s^{2p}\,e^{rs^2})$.

This was shown by FINNEY (1941) to equal

$$\left.\begin{aligned} &E\{s^{2p}\,e^{rs^2}\}= \\ &\frac{(n+1)(n+3)+\cdots(n+2p-3)\,\sigma_x^{2p}}{(n-1)^{p-1}} \\ &\times\left(1-\frac{2r\sigma_x^2}{n-1}\right)^{-\frac{1}{2}(n-1)-p}. \end{aligned}\right\} \quad (6.6)$$

Using this identity we get

$$\left.\begin{aligned} &E\left\{e^{2.303\,\bar{x}+2.652\,s^2}\left(\frac{n-1}{n}\right)[1+bs^4+cs^6+\cdots]\right\} \\ &=e^{2.303\,\varepsilon+\frac{1}{2}\lambda}\left[(1-\lambda)^{-\frac{(n-1)}{2}}+\frac{b(n+1)\,\sigma_x^4}{n-1}(1-\lambda)^{-\frac{(n+3)}{2}}+\frac{c(n+1)(n+3)\,\sigma_x^6}{(n-1)^2}(1-\lambda)^{-\frac{(n+5)}{2}}+\cdots\right] \\ &\text{where} \\ &\lambda=\frac{5.304\,\sigma_x^2}{n}. \end{aligned}\right\} \quad (6.7)$$

Finally by expanding this bracket, and choosing values for $b$, $c$, etc. so as to generate successive terms in the expansion of $e^{\frac{(n-1)\lambda}{2}}$, we get

$$b=\frac{-7(n-1)^2}{n^2(n+1)};\quad c=\frac{50(n-1)^3}{n^3(n+1)(n+3)}$$

so that by ignoring terms of order $s^8$ or more, (6·7) becomes

$$\left.\begin{aligned} &e^{2.303\,\bar{x}+2.652\,s^2}\left(\frac{n-1}{n}\right)\left[1-\frac{7(n-1)^2s^4}{n^2(n+1)}+\right. \\ &\left.\frac{50(n-1)^3s^6}{n^3(n+1)(n+3)}\right]=m \text{ say} \end{aligned}\right\} \quad (6.8)$$

The expectation of $m$ will then be approximately equal to

$$e^{2.303\,\varepsilon+2.652\,\sigma x^2}$$

Therefore, from (6) we may use $m-a$ as an unbiased estimate of $\mu$. If this is called $\bar{\mu}$.

$$\left.\begin{aligned} &\bar{\mu}=e^{2.303\,\bar{x}+2.652\,s^2}\left(\frac{n-1}{n}\right) \\ &\times\left[1-\frac{7(n-1)^2s^4}{n^2(n+1)}+\frac{50(n-1)^3s^6}{n^3(n+1)(n+3)}\right]-a. \end{aligned}\right\} \quad (7)$$

## 5.

# The Sampling of Demersal Fish Stocks by Trawls and Seines.

*By* A. R. Margetts

The following remarks accompanied by examples from fishing experiments over the past few years are set down to illustrate how closely similar or widely different can be the samples of demersal fish obtained from the same fishing ground at the same time by two different fishing gears. The experimental results presented are almost the raw data collected and no attempt is made to apply any rigorous statistical treatment. Published work by Barnes and Bagenal (1951) and Parrish (1951) include detailed statistical treatments of data from single experiments of the type referred to here.

Barnes and Bagenal used one trawler fishing one ground with gear unaltered and examined the haul to haul variation of catches. They found the coefficient of variation for quantities of catches to vary between 40 % and 85 % and concluded that the catches of a given species from two separate hauls could not, on this basis, be considered significantly different unless one was less than a third or greater than three times the other. Such results were obtained on an inshore ground with a trawl having a 54 ft. headline. Care was taken to fish the same ground each haul but, even so, one haul was slightly off the marks and produced very different catches from the other three made immediately after. The experiment also shows how, with the passage of time, species of fish appear, disappear, and reappear on the one ground within a matter of days or even hours. Trawlermen know well how tightly grouped some species of fish may be and, furthermore, how some species, for example rays, appear to be quickly dispersed by trawling; such a time-effect on sampling must not be ignored when sampling a ground with one ship.

In the selected experiments to be referred to below, two or more ships took part; the ships fished for several days as close together as was conveniently possible, hauling and shooting their gear more or less simultaneously and each trawler towed at its optimum speed. Some of the results have been published previously (Margetts (1949), Parrish (1949), and Graham (1954)) but generally with a construction different from the present one.

All the experiments were made primarily to show the relative overall fishing powers of the ships and gear and to show how the gears selected especially the sizes of fish. But many of them reveal rather striking selections of fish species which must be attributable to the action of the gear used in relation to the behaviour of the fish.

### Experimental results.

In two of the experiments the two trawlers "Sir Lancelot" and "Platessa" fished together (Margetts, 1949). The trawls used were almost identical in every respect except size. "Platessa" used a 62 ft. headline trawl while "Sir Lancelot", the bigger ship, used an 80 ft. headline trawl, a scaled-up version of "Platessa"s of the same shape and with the same accessories, all parts and fittings of the larger trawl being proportionately larger than those of the smaller trawl; the cod-end mesh size was, however, the same for both trawls. This experiment was carried out twice, in different years on different fishing grounds, and, considering just total quantities of each species caught in unit time, it was apparent that the larger trawl regularly outfished the smaller on each species of fish, and that the catches of each trawl seemed to be in proportion to the working width of gape of the trawl. These results are shown in Table 1.

**Table 1. Ratios of Catches per Unit Fishing Time, "Sir Lancelot": "Platessa", 1947 and 1948.**

| Species | 1947 (by weight) | 1948 (by nos.) |
|---|---|---|
| Plaice | 1·3 | 1·3 |
| Sole | 1·3 | 1·3 |
| Turbot and Brill | 1·2 | — |
| Skate and Rays | 1·7 | — |
| Dab | 1·4 | 1·0 |
| Gurnard | 1·8 | 0·6 |
| Whiting | — | 1·5 |

Most of the results were for flatfish and were therefore as might have been reasonably expected by assuming that the two trawls were equally efficient in sweeping up the fish on that area of the sea-bed that they covered. That the ratio for the roundfish, whiting, was somewhat above the 1·37 of the width of gape ratio also seems reasonable, as this figure might

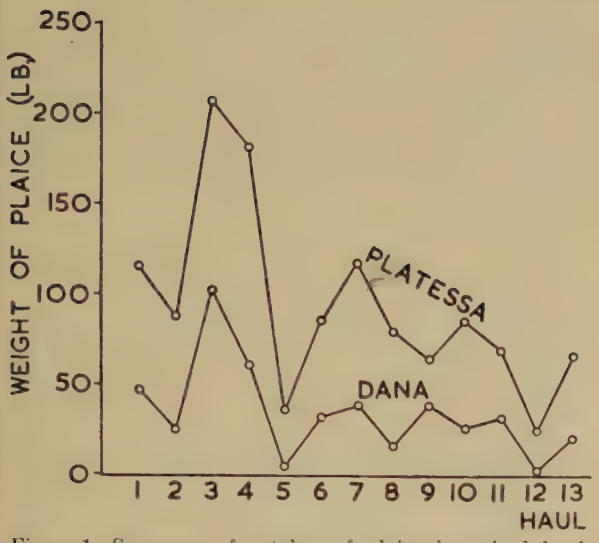



Figure 1. Sequence of catches of plaice in paired hauls by trawlers "Dana" and "Platessa".

well depend upon the frontal area of the trawl mouth opening. But the results for gurnards were definitely odd, the larger trawl catching nearly twice as many as the smaller in one experiment but only half as many in the next experiment; the explanation of this is not readily apparent, especially as in both experiments the ratio of catches of gurnards was reasonably consistent from haul to haul.

When "Platessa", using her normal gear as in the experiment with "Sir Lancelot", trawled against "Dana" using a slightly smaller trawl designed for experimental fishing purposes, flatfish were the most numerous fish on the ground, and on these "Platessa" outfished "Dana" by more than the headline length ratio; the use of a tickler chain by "Platessa" was probably responsible for some of the difference, suggesting that a trawl without a tickler chain failed to catch quite a lot of the flatfish in its path. This experiment provided good illustration of how consistent from haul to haul can be the trawl catches of two vessels fishing together. (Figure 1).

In Figure 2 are illustrated the catches from haul to haul of plaice taken by the two sister ships "Platessa" and "Kirkley" fishing fairly close together over a rather wide expanse of fishing ground. The trawls used were almost identical in design and size, yet in the first five hauls "Kirkley" outfished "Platessa" and especially in hauls 6 to 14 when "Platessa" worked without a tickler chain. From haul 15 onwards, "Kirkley" used a fresh trawl and "Platessa" refitted the tickler chain; their catches were then more similar, "Kirkley"s falling appreciably in hauls 15—17 when the tickler chain was broken.

In each of the above experiments the proportions of each species in the catch at each haul by each ship remained very approximately the same, with the exception of the gurnards in the "Sir Lancelot"—"Platessa" comparison, variations of the gear affecting chiefly the quantities rather than the type of fish caught.

In an experiment comparing the two trawlers "Sir Lancelot" and "Luda Lord" there is evidence of the comparative efficiencies of the trawls differing with the species of fish. Table 2 summarizes the total catches. The ratios of total catches of each species were those that prevailed from haul to haul. There was an 8 mm. difference in cod-end mesh size, that of "Luda Lord" being the larger, but this affected only the whiting results appreciably, there being large quantities of whiting present of a size between the 50 % selection lengths of the two meshes. Otherwise the gears were rather similar, "Sir Lancelot"s trawl having an 80 ft. headline and "Luda Lord"s a 72 ft. headline; the most obvious difference between the gears was that whereas "Luda Lord" used a rubber disc groundrope heavily chained and with heavy tickler chains between Dan Lenos and across the bosom, "Sir Lancelot" used a groundrope of wire heart wound with rope and not so heavily chained, and a single lighter tickler chain. Clearly "Luda Lord" was outfishing "Sir Lancelot" on flatfish but was not catching so many haddock as was "Sir Lancelot". This leads to the supposition that there were essential differences between the actions of the two gears.

**Table 2. Total Catches, by Numbers, from 31 Pairs of Hauls by Trawlers "Sir Lancelot" and "Luda Lord".**

| Species | "Sir Lancelot" | "Luda Lord" | "Sir Lancelot" "Luda Lord" |
|---|---|---|---|
| Plaice | 760 | 2,158 | 0·4 |
| Turbot | 45 | 127 | 0·4 |
| Sole | 24 | 169 | 0·14 |
| Lemon Sole | 94 | 91 | 1·0 |
| Haddock | 1,410 | 712 | 2·0 |
| Whiting | 2,446 | 403 | —*) |
| Cod | 876 | 850 | 1·0 |

*) mesh selection operating.

Such trawl selectivity was shown when the two steam trawlers of equal size, "Sir Lancelot" and "Explorer", fished together on a predominantly roundfish ground, with each ship using its normal trawl

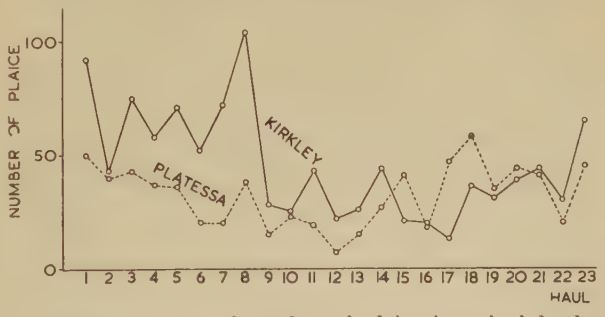



Figure 2. Sequence of catches of plaice in paired hauls by trawlers "Platessa" and "Kirkley".

which was typical of that used in their home ports Lowestoft and Aberdeen except that only "Sir Lancelot" and not "Explorer" used V.-D. bridle gear (MARGETTS, 1949, and PARRISH, 1949). In this case it was "Explorer" that caught far more roundfish (haddock and whiting) than did "Sir Lancelot" while "Sir Lancelot" caught more of the flatfish—the opposite result from that of the "Sir Lancelot"—"Luda Lord" comparison as judged by "Sir Lancelot"s ability to catch roundfish. "Sir Lancelot" also caught a lot more benthos than did "Explorer". In fact, a glance at Table 3 would give the erroneous impression that "Sir Lancelot" and "Explorer" had not fished the same grounds at all.

**Table 3. Total Catches, by Numbers, from 7 Pairs of Hauls by Trawlers "Explorer" and "Sir Lancelot".**

| Species | "Explorer" | "Sir Lancelot" | "Explorer" : "Sir Lancelot" |
|---|---|---|---|
| Whiting..... | 547 | 28 | 19·5 |
| Haddock..... | 1,447 | 547 | 2·6 |
| Cod ..... | 75 | 78 | 1·0 |
| Lemon Sole .. | 23 | 38 | 0·6 |
| Plaice..... | 24 | 56 | 0·4 |
| Angler ..... | 48 | 97 | 0·5 |
| Rays ..... | 19 | 232 | 0·1 |

Consideration items of of gear that would cause one trawl to fish closer to the bottom than the other, as would seem to be happening in the above experiment, led to the repetition of the experiment on flatfish grounds with some hauls made with and some without tickler chains (PARRISH, 1951). This showed the Lowestoft trawl to be far more efficient at catching flatfish than the Aberdeen trawl when both were without tickler chains, but that when both trawls were fitted with ticklers the catches, at least of plaice, were more equal.

When trawlers have fished against seiners the species composition of the catches have been very different. From experimental results (MARGETTS, 1949) it was estimated that over a standard 24 hour period the Danish seiner "Arabis" caught 2·8 times as many plaice as the trawler "Platessa" and 1·7 times as many as the larger trawler "Sir Lancelot" using V.-D. bridle gear. However, while the species composition of the two trawlers' catches was much the same, it was noted that the trawlers caught relatively far more soles, anglers, and turbot and brill than did the seiner. It was also roughly estimated that the area of sea-bed fished by the seiner, taken as the area swept by warps and net, was about 3 times that covered by "Platessa"s trawl in the same 24 hour period, indicating that the efficiencies of the two gears, as judged by their abilities to catch so many fish per unit area of ground, were approximately the same on plaice, but that the trawl was more efficient for catching such species as sole.

The foregoing examples illustrate how, all other things being equal, the quantitative catches of two trawls depend upon the sizes of trawls ("Sir Lancelot"—"Platessa"); how this quantitative relationship is disturbed by variation of small items of gear ("Platessa"—"Kirkley" and "Sir Lancelot"—"Luda Lord"); and the differential efficiency of any gear between species present together on the ground ("Sir Lancelot"—"Luda Lord", "Sir Lancelot"—"Explorer", and trawler-seiner).

Finer differences are encountered in the size selection of fish by the various ships and gears. The majority of cod-end mesh selection experiments have been made with trawlers' double sisal or manila cod-ends, and these results, from various sources, have generally fitted into a logical sequence, a peculiarity of which has tended to be that larger meshes catch more of the larger fish; this suggests a selectivity of the trawl secondary to that determined by whether a fish can or cannot pass through the mesh. In the "Sir Lancelot"—"Luda Lord" comparison it appeared as though, for at least some of the time of the experiment, "Luda Lord", besides catching more plaice, actually caught more of the very large plaice, perhaps rather more than was due to her larger mesh alone. Similarly, in the first "Sir Lancelot"—"Explorer" comparison there was the suggestion that "Sir Lancelot", although catching many fewer haddock, caught rather more of the large haddock than did "Explorer" ("Explorer" caught 1,262 haddock of length 31—44 cm. as against 406 by "Sir Lancelot", but only 61 of length 45—56 cm. as against 88 by "Sir Lancelot") while both trawls were fitted with cod-ends of approximately the same mesh size. Subsequently, by means of underwater photography of trawls in action, the fishing shapes of these two trawls have been discovered; "Explorer"s net without floats and V.-D. bridles had a wide spread but small vertical gape, and "Sir Lancelot"s with floats and V.-D. bridles had a relatively small spread but much higher vertical gape. This would support the suggestion that "Sir Lancelot" caught more big haddock because they were swimming rather higher off the bottom than were the smaller ones.

A further example of differential size selection operating above the range of actual mesh selection is provided by the "Platessa"—"Arabis" and "Sir Lancelot"—"Arabis" trawler-seiner comparisons (MARGETTS, 1949). The ratios of catches, seiner to trawler, at each centimetre length-group of plaice above the seiner's mesh selection range were approximately constant for "Sir Lancelot"—"Arabis", but those for "Platessa"—"Arabis" were ever-increasing. This indicates a failure of "Platessa" to catch some of the larger fish which the seiner and the bigger, and somewhat faster towing, "Sir Lancelot" were catching.

The fishing of the fly-dragging seiner "Elizabeth Crawford" against the trawler "Platessa" on roundfish grounds (GRAHAM, 1954) was one of several English and Scottish experiments which showed that with the same size of cod-end mesh the fish size selection of the seiner was noticeably higher—about 12 % for the sizes investigated—than that of the

trawler. It had previously been suggested as a result of Danish seiner-trawler trials (Margetts, 1949) that parts of the seine gear other than the cod-end mesh might affect the size selection of fish. Recently, trawling experiments (data submitted to I.C.E.S. Permanent Commission Liaison Committee) have shown that differences in the material used in making a trawl cod-end affect its selectivity.

**Conclusions.**

(1) The quantitative efficiencies of trawls in catching fish in their path vary considerably with apparently minor modifications of the trawling gear.

(2) Trawls of different design and different rigging, and seines, show marked differential selectivity among species of fish on a ground.

(3) Size selection of fish by trawls and seines depends not only on the size of mesh but also upon the material that is used in making up the net and perhaps also to some extent upon the action of the gear as a whole.

**Discussion.**

If the experimental findings do in fact hold true in commercial fishing, then, when comparing catches of fish from areas, each of which is fished chiefly by one type of trawler with a characteristic gear, the extent of species selection by the gear should be borne in mind. For example, although it is a biological fact that there are more haddock in the northern North Sea than in the southern North Sea, and vice-versa for plaice, a direct quantitative comparison of densities of each species, as measured by catch per unit effort, would be misleading when the northern North Sea is fished by trawls especially efficient on haddock and inefficient on plaice and when the southern North Sea is fished by trawls more efficient on plaice but less efficient on haddock; a distorted picture of true densities would be obtained. But, for most practical purposes, so long as there were no marked changes in the fishing distribution of the northern and southern trawling fleets, the record of commercial catches can be safely used for stock analysis and population studies. It is very likely that the density of haddock towards the southern fringe of its North Sea distribution is shown by commercial fishing statistics as being lower than it actually is, and that similarly the commercial statistics show the density of the northern North Sea plaice as lower than it actually is.

In any experimental trawling or any sample trawling for the collection of data which may be compared with that collected by another ship, it is most essential that a complete record be kept of full details of all parts of the trawl and its rigging, including such apparently trivial items as type of twine used, and of how the trawl was worked, e. g., speed of towing, and warp length used. The phrase 'normal trawl' is virtually meaningless in sampling comparisons.

The species and size selectivities of different trawls, varying as they are shown to do by these experiments, indicate that, in trawling, other features besides mesh also exercise a selective effect on catches; it is not impossible that such selection may be differential throughout a size range of fish.

Knowledge of the behaviour and action of fishing gear and of fish behaviour is far from complete, but it has been notably advanced in recent years and will undoubtedly be improved in future. The value of many sampling records will be increased in future with increase in knowledge of gear action and fish behaviour, but only if it is known exactly with what gear the samples were taken.

## 6.

# A Discussion of some Limitations of the Trawl as a Sampling Instrument.

*By* R. Jones

### Introduction.

The problem of sampling fish populations is one that has raised many difficulties during the past fifty years. The major sampling objectives of eliminating bias and minimizing variance have been referred to by Parrish in his contribution to this symposium and will only be briefly mentioned below. In general, variance (e. g., the variations in numbers of fish taken in replicate trawl hauls) tends to be large, but can be minimized by making a sufficient number of hauls according to a properly planned sampling programme. Bias on the other hand can sometimes arise without the investigator's knowledge. This might be due to:—

(a) An imperfect knowledge of the way in which the sampling gear behaves, (b) unreliable sub-sampling methods, (c) an imperfectly planned sampling programme, (d) unsound methods of analysis.

The fact that no sampling gear is perfect, in the sense that all have limitations that cannot always be allowed for, is no new discovery. Kyle (1903) pointed out that different fishing gears could give very different estimates of the relative abundance of different species on the same ground, and Davis (1934) emphasized that no trawl-net gives a representative picture of the entire population on any ground. Right from the start, it was appreciated that lines, trawls, and later seine-nets, were limited as sampling instruments in the following respects:—

(a) All are selective. For example, Margetts (1948) showed that the addition of a tickler chain to a trawl led to a disproportionate increase in the catches of flatfish, and Parrish (1948 and 1951) showed that a round-fish trawl caught proportionately more round-fish and less flatfish than a flatfish trawl.

(b) It is not possible to determine the absolute density of any species by direct sampling, since there is no estimate of the proportion of the available population that is taken by any gear.

This was fully appreciated by Russell (1931), as well as by many others. Russell pointed out, however, that this consideration need not prevent a gear being used for comparative purposes, provided it always catches the same proportions of each species in its path when worked under constant conditions. It should then be possible to compare the densities of any species in two regions or at different times without knowing its absolute density in either case.

This paper discusses some of the limitations of the trawl as a sampling unit, so that in due course allowance can be made for them in the interpretation of results. For example, if a haul is made with a commercial trawl or seine, some selection of the catch will take place by the escape of small fish through the cod-end meshes. A sample collected in this way, although biased as regards its size composition, need not cause the investigator to arrive at false conclusions provided this factor is allowed for; for example, if the selection characteristics of the cod-end in use were first determined.

### The effect of duration of haul on catch.

On several occasions during the past three years comparative tests of the effect of duration of haul on catch have been made by Scottish research ships. In each instance a test was carried out to determine whether doubling the duration of a haul doubled the catch of fish or not. For statistical purposes the analyses were carried out on the differences of the logarithms of the numbers caught in each series of hauls. These differences, together with their standard errors, are shown in Table 1.

On the simple assumption that a 2 to 1 ratio in the catch is to be expected by doubling the duration of a haul, it is the deviation of these means from log 2 (·3010) that is to be tested.

In the June 1951 experiments it was found that the increase in the catches of flatfish, and also all species taken together, differed significantly from a 2 to 1 ratio. In the later experiments the results were non-significant although, with the exception of lemon sole and in one instance, haddock, doubling the duration

**Table 1. Mean Differences (M. D.) and Standard Errors (S. E.) of the Logarithms of the Numbers of Fish captured in Hauls of different Duration.**

| | Haddock | | Whiting | | *G. esmarkii* | | L. Sole | | Dabs | | Total flatfish | | All species | | Degrees of freedom for testing mean differences |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M. D. | S. E. | M. D. | S. E. | M. D. | S. E. | M. D. | S. E. | M. D. | S. E. | M. D. | S. E. | M. D. | S. E. | |
| June 1951 | | | | | | | | | | | | | | | |
| 1½ hour v. 3 hour | ·215 | ·048 | — | — | — | — | — | — | — | — | ·105 | ·074 | ·185 | ·047 | 16 |
| May 1953 | | | | | | | | | | | | | | | |
| ½ hour v. 1 hour | ·208 | ·052 | ·220 | ·098 | ·152 | ·082 | ·345 | ·088 | ·184 | ·072 | ·187 | ·066 | ·166 | ·066 | 11 |
| Dec. 1953 | | | | | | | | | | | | | | | |
| ½ hour v. 1 hour | ·156 | ·110 | ·070 | ·216 | — | — | — | — | — | — | ·199 | ·179 | ·048 | ·161 | 3 |
| May 1954 | | | | | | | | | | | | | | | |
| ½ hour v. 1 hour "Kathleen" | — | — | — | — | — | — | — | — | — | — | ·200[1]) | ·047 | — | — | 18 |
| May 1954 | | | | | | | | | | | | | | | |
| ½ hour v. 1 hour "Explorer" | ·325 | ·079 | — | — | — | — | — | — | — | — | ·270[1]) | ·111 | — | — | 18 |

[1]) In this experiment, the "flatfish" were Plaice.

of the haul gave consistently less than twice the catch.[1])

We cannot yet exclude the possibility that these results were due to chance, although in view of these considerations this would appear unlikely. The most interesting feature of these results is that, from certain assumptions, one might have expected that by doubling the duration of a haul more than twice the number of fish might have been caught for the following reason:—

The research film "Fish and the Seine-Net" shows that, during hauling, plaice are herded along in front of the groundrope, but that from time to time an individual falls "out of line" and drifts back into the net. It seems reasonable to extend these results to trawling for other species also, and to suppose that there would be a gradual accumulation of fish in front of the groundrope as the haul progressed. For all that, the longer a fish is herded in front of the footrope, the more likely it is to be ultimately captured. This being so, it follows that with an increase in the number of fish accumulated in front of the net there would be a proportionate increase in the number of fish entering the net per unit time. In other words, more fish would be captured, on the average, during the second half of a haul than during the first half. For these reasons, doubling the duration of a haul might be expected to lead to more than a doubling of the catch.

There is no doubt that the results in Table 1 differ consistently and in several cases significantly from those expected on this reasoning, and the really interesting question is: "why should there be such a discrepancy?" Three possible answers to this question will be discussed below:—

(a) It is possible that when a fish such as a plaice is disturbed by a footrope, it either enters the net, or swims "indefinitely" in front of it. While this seems unlikely, something like this does seem possible in the case of roundfish such as haddock or whiting. The effect of a net might then be to scare a shoal so that some individuals were instantly caught, while the rest escaped completely from the influence of the net. Even if this should prove to be the case, however, it follows that the rate of capture would at least be constant throughout a haul.

(b) As the cod-end tends to fill up with fish, the waterflow through the net might be reduced, leading to an overall loss in the rate of capture of fish. This could arise because of an increase in the quantity of water being "pushed in front of the net", away from which fish might be expected to swim. This seems a reasonable hypothesis, but is is difficult to reconcile with the results obtained from mesh selection experiments when alternate hauls have been carried out with and without a small mesh cover. If, as suggested, a reduction in the waterflow through the cod-end can cause a serious reduction in the catch of fish then it would be expected that the presence of a small mesh cover over the cod-end would tend to produce such an effect. In fact, most of the results obtained by this laboratory (Parrish and Pope, 1951), as well as those obtained by the United States Fish and Wildlife Service in their haddock investigations (Clark, 1952) show no significant difference. There is little reason to suppose, therefore, that the reduction in the waterflow through the cod-end due to the presence of fish in the cod-end would become serious until the catch were large.

(c) An alternative explanation is that a group of fish swimming in front of the footrope might scare fish well in front in the path of the trawl, so reducing the likelihood of these individuals entering the net. In that case, the preliminary accumulation of fish in front of the net might ultimately lead to the loss of

[1]) A further experiment in which a wider range of durations were compared, was undertaken by F.R.S. "Explorer" in September 1954. Hauls of half, one, two and three hours were made and a relationship of the form —catch $\alpha$ (duration)$^x$ was fitted to the results. The coefficients '$x$', which should have been equal to unity if the relationship was strictly proportional, were found to equal 0·7885 and 0·5919 for haddock and whiting respectively. The haddock coefficient (0·7885) was found to differ significantly from unity at the 5 % level but, owing to a very high error variance, the whiting coefficient did not.

**Table 2. Numbers of four-year and older Faroe Haddock taken by "Scotia" and by Aberdeen Trawlers, expressed as Percentages of the Numbers of three-year-olds.**

| Age | 1950 | | 1951 | | 1952 | | 1953 | |
|---|---|---|---|---|---|---|---|---|
| | Commercial | "Scotia" | Commercial | "Scotia" | Commercial | "Scotia" | Commercial | "Scotia" |
| | % | % | % | % | % | % | % | % |
| 4..... | 51 | 6 | 19 | 8 | 58 | 20 | 59 | 24 |
| 5..... | 49 | 23 | 4 | 3 | 7 | 2 | 23 | 14 |
| 6 and older.. | 30 | 28 | 28 | 15 | 16 | 6 | 15 | 6 |

fish and a falling off in the rate of capture during the course of a haul.

If (c) should prove to be a correct or partial explanation, it might lead to some very interesting conclusions regarding the effect of population density on catch for which ultimately due allowance would be made when interpreting results. Whatever the explanation, however, it would appear that these results warrant further investigation. In this manner, new light may be thrown on the behaviour of fish on the approach of a trawl and due allowance made for any anomalies thereby produced.

### A comparison of age compositions from commercial and research ship catches.

A second example of considerable interest arises from a comparison of the age compositions of research ship and commercial samples taken from the same areas.

From 1950 onwards, extensive sampling of the haddock population at Faroe has been carried out by F.R.S. "Scotia". At the same time, estimates of age composition and catch/unit effort of different broods have been made from commercial data by intensive sampling on the Aberdeen fish market. The point that concerns us here is a comparison of the age composition of the stock obtained by these two methods. In order to eliminate any mesh selection (or deliberate rejection) effects, all haddock of less than three years of age (i. e., less than about 38 cm. in length) were excluded from the comparison. The numerical estimates of the broods older than three years were then expressed as percentages of the numbers of three-year-olds in each sample and these results are presented in Table 2.

In every instance, there were proportionately fewer old fish in the "Scotia" samples than in the commercial samples. There are two possible explanations of these results:—

(a) There was a selective difference between the gears used by commercial trawlers and "Scotia".

(b) Aberdeen trawlers spent relatively more time in fishing those spots where the older haddock abounded. "Scotia" sampling on the other hand was more or less random.

A further set of comparisons of a similar nature was made between market sample results and "Explorer" data from the North Sea. In this case, comparisons were only made when the commercial ship concerned was known to have been fishing in one locality only, and that "Explorer" had fished within about fifteen miles of it during the same period. The market sampling involved only measuring the haddock and so, instead of dealing with age composition, the numbers of haddock of 38 cm. and over and 41 cm. and over have been expressed as percentages of those of 31 cm. and over in each case. These results are presented in Table 3.

**Table 3. Numbers of Haddock of different Sizes, expressed as Percentages of the Numbers of 31 cm. and over.**

| Area | Date | 38 cm. and over | | 41 cm. and over | |
|---|---|---|---|---|---|
| | | Commercial | "Explorer" | Commercial | "Explorer" |
| | | % | % | % | % |
| C14 | Jun. 1952 | 35 | 22 | 12 | 33 |
| D12 | Sep. 1952 | 50 | 0 | 20 | 0 |
| D13 | Sep. 1952 | 43 | 0 | 19 | 0 |
| C12 | Jan. 1953 | 19 | 6 | 10 | 0 |
| C14 | Jan. 1953 | | 4·5 | | 0 |
| C12 | Mar. 1953 | 62 | 24 | 53 | 16 |
| C13 | Sep. 1953 | 13 | 6 | 6 | 1·4 |
| C11 | Oct. 1953 | 26 | 23 | 9 | 2 |

(In all of these comparisons there is the difference that "Explorer" made one or more hauls in the same place, whereas the commercial ship had spent a whole trip in one general vicinity.)

In only one case, out of the sixteen, did "Explorer" catch proportionately more old fish than a commercial trawler.

During September 1953, an experiment of particular interest was carried out which took the form of a direct comparison of a research ship (F.R.S. "Explorer") and a commercial trawler (S.T. "Viking Prestige") fishing side by side. The experiment was carried out over a period of two weeks. The nets fished by the two vessels were of the same general dimensions, but "Viking Prestige" worked with 30 fathom V.-D. sweeps, and "Explorer" without sweeps. The size compositions of the haddock sampled are shown in Table 4. Two sizes of mesh were used during this experiment (70 and 80 mm.) but to exclude any small difference in mesh-size between the two ships the numbers of haddock of 35 cm. and over and 40 cm. and over have been expressed as percentages of the numbers of 31 cm. and over in each instance.

**Table 4. Numbers of Haddock of different Sizes, expressed as Percentages of the Numbers 31 cm. and over.**

| | | "Explorer" | | "Viking Prestige" | |
|---|---|---|---|---|---|
| | | 35 cm. and over | 40 cm. and over | 35 cm. and over | 40 cm. and over |
| 1st week | 70 mm. mesh | 33 | 9 | 15 | 0 |
| | 80 mm. mesh | 30 | 8 | 32 | 9 |
| 2nd week | 70 mm. mesh | 19 | 2 | 18 | 4 |
| | 80 mm. mesh | 16 | 3 | 13 | 1 |

**Table 5. Average Numbers and Percentages of Haddock, Cod and Lemon Sole per Hours' Fishing in 4 Day and 5 Night Hauls.**

| | Haddock | | | Cod | Lemon Sole |
|---|---|---|---|---|---|
| | 1-yr.-olds | 2-yr.-olds | 3-yr.-olds an older | | |
| Day ... | 51 | 21 | 2·2 | 2·0 | 0·5 |
| (%) ... | (69) | (28) | (3) | | |
| Night.. | 108 | 204 | 39 | 9·0 | 12·5 |
| (%) ... | (31) | (58) | (11) | | |

It is quite clear from the results in this table that the commercial trawler was not catching a greater proportion of large haddock than the research ship on this occasion. As far as this evidence is concerned it would appear that the differences in age composition between commercial and research ship samples were not so much a gear effect as the result of a tendency for commercial trawlers to concentrate on those spots where larger haddock are to be found. If this should prove to be the explanation, then it would have one or two interesting consequences that should certainly be investigated. For one thing, if commercial age compositions contain a disproportionately large number of old haddock (and possibly other species too), then any estimates of survival rate made from commercial data will tend to be overestimated to some extent. Also, in making equilibrium yield/effort calculations it is usual to assume that fishing mortality is constant with age. If commercial ships tend to concentrate on large haddock, however, then fishing mortality will increase with age, and a recalculation of the effects of mesh and effort changes, allowing for such a factor, will be required.

At present insufficient is known of the action of trawls to exclude the possibility of a real gear effect as the explanation for the age composition discrepancies. The possibility of a "sweep" effect has been tested, however, both by "Explorer" and "Viking Prestige", and also by "Explorer" alone, in May 1952. In each case there was nothing to suggest that the use of sweeps affected the age composition of haddock. Other differences, such as speed of towing, and the warp length/depth ratio for instance still remain, and are being investigated. Only when these have been tested and eliminated will it be possible to settle this problem with any degree of confidence.

### The day and night fishery at Faroe.

It is common knowledge amongst trawlermen fishing in Faroese waters that, from about October to the end of April, better catches are generally to be obtained during the hours of darkness than during daylight. This was confirmed by data obtained during trawling experiments by F.R.S. "Scotia" in April 1951. In addition to routine trawling at different positions, nine replicate hauls spread over three 24 hour periods were carried out at a position off the island of Nolsø in statistical square XX22b.

The results of these experiments were very striking and are shown in Table 5.

With the exception of the one-year-old haddock catches, the numbers of all species taken at night were significantly higher than those taken during the day. This experiment was carried out over a period lasting three days, during which there was no indication of any depletion in the numbers of fish on the ground sampled. It is evident that, as well as an increase in number, the proportion of old haddock caught at night was larger than during the day.[1]) The difference observed for haddock was highly significant and clearly suggests that the availability of haddock may not only vary with time, but also with age. It is possible that, during daytime, there was a tendency for the larger haddock to leave the bottom and so evade capture, in which case the trawl may still have given a representative picture of the age composition of haddock near the bottom. Whether lemon soles leave the bottom or burrow more deeply during the daytime is not known.

The importance of this result is that it once more emphasizes the need for careful planning in any survey. In such an instance, when the diurnal cycle is comparatively regular, due allowance can be made when using the trawl for comparative purposes. In that case, comparisons should all be made at about the same time of day or, better still, would be made both by day and by night, provided a sufficient number of each were made to allow for any diurnal effect.

## Summary.

In any sampling programme, it is essential that the work is planned with a view to minimizing variance and eliminating bias. By far the greatest difficulties are presented by the latter since bias can only be completely allowed for, if every limitation of the working of the sampling gear is known and can be allowed for. In this respect the fisheries biologist is at a disadvantage compared with, say, the agricultural scientist, since the investigation of the limitations of the trawl as a sampling instrument presents a particularly difficult problem. For this reason, it is necessary to make certain assumptions about the way in which a trawl works. Such assumptions are, of course, merely temporary and are meant to stand until replaced by something better. In this contribution an attempt has been made to question the validity of some of these assumptions on the basis of experimental evidence, and to indicate the ways in which they might ultimately be modified in the light of further research.

[1]) This result is of the same type as that arrived at for herring by Lucas (1936) on a re-examination of data collected by Fulton (1922). He found that young herring were proportionately fewer in trawl catches taken by night than by day, which in general are less heavy than those taken by day.

7.

# Sampling Problems in Fish Population Studies, with Special Reference to North Sea Herring Investigations.

*By* B. B. Parrish *and* G. McPherson

## PART I

## Some Basic Sampling Problems.

### Introduction.

Apart from the very rare occasions when complete population censuses are possible, marine fish population studies must be based on sampled data. Sampling techniques are fundamental to investigations in this field, and the accuracy and validity of the results will largely depend on the use of efficient sampling methods. It is of great importance, therefore, that full consideration should be given to the sampling problems which arise at all stages in such investigations, and that sampling methods should be adopted which provide the most efficient estimates of the required population parameters within the limits set by the available resources of money, manpower, time and equipment.

### Sources of Error, and Basic Sampling Aims.

Whatever the objective of an investigation, the inaccuracies which may arise from the application of sampling techniques are of two main types, (1) systematic error (bias), and (2) random error. Biased sampling gives rise to estimates of the population parameters which are higher or lower than the true value for the population, and random error limits the precision with which the true value of the parameter can be estimated. Clearly, it should be the aim in the design and execution of all sampling programmes to eliminate systematic error and to minimize random error.

#### 1. Systematic error.

Systematic error may arise from a number of different causes and at different stages in the execution of a sampling programme. However, it can usually be traced to one of three basic sources.[1]) These are:—

(a) The sampling gear;
(b) Sub-sampling methods;
(c) Time and spatial distribution of samples.

Sources (a) and (b) may affect the accuracy of each sample that is taken but (c) will affect the results of the sampling programme as a whole.

Of these sources, (a) presents the most formidable problems. Whereas biased estimates of the population parameters due to (b) and (c) can usually be avoided by the adoption of properly designed sampling programmes and sub-sampling techniques, it is sometimes very difficult or impossible to ensure that the sampling gear provides completely unbiased samples of the population present at the times and places at which they are taken. It is indeed sometimes difficult to measure the magnitude or direction of the inherent bias, due to the absence of an ideal standard against which to test the efficiency of the gear in use.

**(a) The sampling gear.** The ideal gear is one which provides a completely representative sample of the particular population variate of which an estimate is required, but in practice the nature of the sampling demands will vary according to the main objective of the investigation. Two main types of investigation arise. In the first, which includes growth studies, racial investigations, food investigations etc., the basic sampling requirements are representative samples of the distribution of the variates (length, age, vertical number, stomach contents etc.) in the population at each sampling locality. In these investigations the relation between sample size and the total number of fish in the population is not important. In the second type, which includes all investigations in which comparable estimates are required of the absolute and relative numbers of individuals in the population in different areas and at successive intervals of time (e. g., mortality estimations), the demands are greater in that the relation between sample size and population size must be known, or be approximately constant from sample to sample.

It is evident that a gear which satisfies the basic

[1]) A bias may also arise from the use of inefficient methods of analysing the sampled data. This source of bias is not discussed here, but is dealt with in papers presented by Gulland, Pope and Jones to this symposium.

requirements for the first type may not necessarily do so when used in the same manner for the second. For example, seasonal or area changes in the behaviour or distribution of a population of fish may give rise to large variations in the numbers of fish taken by the gear from time and place to place, and so give very different estimates of the population size, but they may not necessarily prevent the collection of representative data of the distribution of variates such as length, vertebral number, etc.

In some investigations, a sampling gear which is known to fall short of the "ideal" standard for the whole fish population may still meet the basic requirements for a stratum of the population. This may be so, for example, for a net which fails to provide representative samples of the small fish in the population due to mesh selection, but which is completely efficient in sampling the larger sizes.

The causes of gear inefficiency fall into the following two main groups:—

(i) Inherent gear selectivity. This group includes the various forms of mesh selection in trawls, seines, gill-nets, etc., and hook selection with lines. The bias which arises from these causes is usually fairly constant in both direction and magnitude, and for some gears it is fairly easily measured. Again such gears may still provide unbiased samples of a known part of the population, and in some cases the selectivity of the gear may be overcome by the use of appropriate accessory gear. A common example is the use of small meshed covers over the cod-ends of otter-trawls.

(ii) Non-uniformity in fish behaviour and habits. This may result in fairly constant differences in availability or catchability between different groups of the population at each sampling locality, or it may result in differences in availability or catchability of the whole or part of the population in different areas and times.

The systematic error which arises from this source of inefficiency is often very difficult to detect and measure because of the difficulties in experimentation. However, some guide to the effects of these factors can be gained from a knowledge of the biology of the species in the sampling area, from the results of direct or photographic observations of the gear when fishing and from comparative fishing experiments with different sampling gears, the general modes of action of which are known.

**(b) Sub-sampling methods.** As with the sampling gear, the ideal technique for sub-sampling the catch when it is too large to be handled is one which provides a completely representative sample of the population variate of which an estimate is required. In this instance the population is not the whole stock, but may be the catch from a single haul, the total landing from a single voyage or the catch of all vessels landing at the port in any period of time.

Pope, in his contribution to this symposium, shows that the ideal sub-sampling technique is one which ensures an equal chance of each fish in the population being selected, and that this is brought about by selecting the members of the sample at random. The ease and certainty with which a random sub-sample can be taken depends upon the degree of segregation, either by accident or design, of the individuals in the population. When the form of the segregation is known, e. g., size categorization at the landing port, the task of taking a sufficiently random sample of the population is relatively easy; but greater difficulties arise from "accidental" segregation which may not be detected readily and yet may be large enough to produce serious bias.

Some examples of possible sources of "accidental" segregation are:—

(i) Segregation of sizes on the deck of a trawler when released from the cod-end.

(ii) Segregation of sizes within the hold of a drifter due to differences in the ease of shaking fish from the nets.

(iii) Differences in sizes of fish in a line of boxes on the landing quay taken from an uncategorized catch, owing to unintentional selection by the fish porters.

A completely efficient method of sub-sampling, which unfortunately is seldom practicable, is to assign a number to all individuals in the population and to select from it a sample of the required size with the aid of a table of random numbers. In practice, this procedure is usually too expensive and time-consuming and some less meticulous method must be adopted. It is because of this need for economy that unsuspected "accidental" segregation may lead to biased sampling. In most instances the form of segregation can only be detected by detailed investigation at the outset of the investigation. Some such preliminary analysis is always necessary if ultimate economy and accuracy is to be achieved.

**(c) Time and spatial distribution of samples.** The biases arising from the sources discussed above apply to the data contained in each sample taken in a sampling programme; a further possible source of bias arises from inefficient spacing or timing of the samples.

It has been shown that differences in habits between groups of individuals at each sampling position may lead to unrepresentative sampling, so, regional stratification of the fish stock within its range of distribution will lead to an unrepresentative aggregate sample unless all strata are included in the sampling programme. Almost all marine fish stocks exhibit some form of area stratification within their limits of distribution, the population variates which are commonly involved being age, length, sex, maturity stage, and abundance. Biased estimates of any or all of these variates may be obtained whenever the sampling programme fails to cover all the strata contained within the territorial limits of the stock.

As in sub-sampling from a stratified catch, the greatest difficulties in planning a sampling programme of a stratified stock will arise when the degree of stratification is unknown or ill-defined. However, it is usually possible to reduce the bias to a minimum in such instances by distributing the sampling effort

approximately at random over the territory occupied by the stock. Again, there are a number of ways in which this can be carried out, depending on local circumstances. Usually the results from initial random sampling surveys will provide information on stock stratification, which will permit the employment of more efficient sampling systems subsequently. The importance of making these preliminary surveys is vital to ultimate accuracy and economy.

One important example of the dangers arising from stock stratification is in sampling from the commercial fishery. Commercial vessels will generally aggregate where the greatest quantities of the best quality fish are available, so that if there is substantial segregation of, say, sizes of fish within the range of distribution of the stock, biased estimates of the mean length of the whole stock will be obtained from sampling the commercial catches alone.

In such instances the deficiencies of the sampling system can be partly remedied by employing a research vessel to sample those strata of the stock not covered by the commercial fishery. Because of the many other advantages of sampling from the commercial catch it is important that the magnitude of the bias arising from non-random coverage of the stock should be investigated at an early stage in the investigation.

A special case of unrepresentative commercial coverage of the entire stock arises when a fishery by one method of capture, or by one country, operates in a section of the territory of a stock which is also fished by a number of other countries and by a variety of gears. In this instance serious bias may arise in estimating stock parameters from the landings of one country or one type of gear only. An example of this type of problem, met in sampling herring in the North Sea, will be given in Part II.

**2. Random error.**

This component of error will usually be determined by one or more uncontrollable factors operating at different stages in the sampling programme. Examples of some of these factors are:—

(1) Small unsystematic haul to haul variations in the efficiency and performance of the sampling gear.
(2) Random variations in the composition of the fish population from time to time and place to place.
(3) Random variations in the sorting methods employed on board ship or on the market.
(4) Personal errors of measurement, etc.

The relative importance of these factors varies greatly from one investigation to another but it is usually possible to assess their importance during the early stages of each investigation.

The objective of all sampling programmes should be to reduce the random error component to a minimum. This can usually be achieved, within the limits set by available resources, by correct planning on a statistical basis.

In addition to the above mainly uncontrollable factors, two controllable factors which also affect the magnitude of the statistical variance (the measure of random error) must be mentioned. They are, the size of sample and the number of samples taken in the sampling programme. Clearly, each should be fixed so as to ensure the smallest variance of the estimated parameter. The statistical principles underlying this choice are given in the contributions by Pope and Gulland, to this symposium.

## PART II

## Sampling Problems in North Sea Herring Investigations.

The extent of the sampling problems and difficulties in fishery investigations will of course depend on the nature of the investigation and in particular on the precision required in the final estimates, and also on the complexity of the structure and habits of the fish population and of the gears which exploit it. Clearly less precautions need be taken in the design and execution of the sampling programme in "qualitative" investigations, for example studies of the limits of distribution of a spawning type or a population variate, than in "quantitative" investigations in which estimates of a variate (e. g., mean length or age) or the absolute or relative numbers of a length or age-group or the whole population are required.

"Quantitative" investigations are growing in importance and urgency in current North Sea herring research. Whereas hitherto the greater part of the research effort has been devoted to the elucidation of the complex biology of the herring populations, greater attention is now being focussed on dynamical studies and the solution of the fishing equation. In consequence, sampling problems and difficulties, which were relatively unimportant in the earlier work, are of major importance at the present time. These concern in particular the elimination of bias in the estimates of the main population parameters which form the basis of dynamical studies.

The number of specific herring investigations in this category in which particular sampling problems and difficulties arise is too large for all to be discussed here. Therefore consideration is restricted to two important sampling problems common to all "quantitative" herring investigations. These are:—

(1) Gear selectivity.
(2) The distribution of sampling effort in area and time.

More specific attention is then paid to the design of sampling programmes for evalutaing the main population parameters of the North Sea autumn spawning stock.[1])

## Gear Selectivity.

Two methods of sampling can be used in investigations of exploited fish populations.

(i) By the employment of research vessels equipped with standard proved gears.
(ii) By sub-sampling from the catch of the commercial fisheries in each region.

The first has the advantage of allowing strict standardization of the gear used and in the design of sampling programmes, while the second is cheaper and permits much more intensive sampling per unit cost. Which of these methods should be adopted will usually be governed by the degree of representativeness of the commercial catch as a sample of the population variate under investigation. This is a very important consideration in current North Sea herring investigations and in planning future investigations which cover more than one fishery. Many data are collected from each of the North Sea herring fisheries in which different gears and methods of operation are employed, but at present it is not possible to compare the data from the different areas. Clearly, a collective assessment of their comparability is urgently required before further co-ordination of the North Sea herring investigations can be effected.

The fundamental questions which arise from this requirement may be expressed as follows:—

(1) What are the absolute selection characteristics of each gear?
(2) How representative of the various population variates are the catches taken by the fisheries in each area?
(3) In fisheries where more than one gear is used, which gear gives the more representative catch —and can the data from the other(s) be of value?

Complete answers to (2) and (3) will show to what extent the commercial catch in each area can be taken as a representative sample of the population and whether regional sampling from the catches taken in the different fisheries is an acceptable method of sampling the North Sea stock, while answers to (1) will incidate which gear should be used in research vessel sampling programmes if the commercial catch proves unacceptable, and will assist in correcting for bias in the data due to inherent selectivity.

So far as the authors are aware, sufficient collective data are not available at the present time to provide complete answers to these questions but some information is available on the selectivity of some of the gears used in the North Sea herring fisheries, and on their representativeness as sampling units at certain places and times. In the following sections consideration is restricted to the two most widely used gears, drift-net and herring trawl.[1])

### 1. The drift-net.

The features of fishing by drift-net, which govern its efficiency, may be summarized as follows:—

(1) It acts as a passive, slowly moving wall of netting into which fish swim and become enmeshed.
(2) It contains no bag or cod-end in which fish are retained.
(3) It covers a relatively narrow stratum of water.

The most important consequence of (1) and (2) is that mesh selection may result in fish being rejected over two sections of the size range of the population, those containing fish with girths too small and too large, respectively, to be held in the meshes; the consequence of (3) is that selection may result if the population exhibits marked depth stratification, or if the depth distribution of the whole population changes markedly from time to time and place to place.

**(i) Mesh selection.** The essential task in describing the absolute mesh selection characteristics of the drift-net and in assessing its reliability as a sampling instrument for any herring population is to determine for each mesh size the critical sizes of fish below and above which rejection operates, and the form of the selection curve over each selection range (for a theoretical treatment of a possible form of drift-net mesh selection see Buchanan-Wollaston, 1927). So far as the authors are aware, no values of these critical sizes for different meshes have been published for the North Sea herring, but there are some published results of comparisons between the catches of drift-nets of different mesh sizes and with other gears. These give some indication of the degree of mesh selectivity of the drift-net in some areas. Relevant information is contained in papers by Delsman (1914), Bjerkan (1917), Borley and Russell (1922) and Hodgson (1927, 1933). These papers, and others dealing with gill-net selectivity of other species are reviewed by Hile (1936). They contain the results of two different methods of approach; in the first, the compositions of the catches taken by drift-nets of different mesh size at the same time and place are compared, and in the second the compositions

[1]) The autumn spawning stock, as defined here, embraces the main body of herring living in the North Sea with spawning grounds ranging from the Shetlands to the English Channel and a spawning season covering the period July to February. It is recognized that this population of herring may contain a number of distinct spawning communities, but in the absence of essential information as to their number, geographical limits, and degree of intermixing, they are considered for the present purpose as a single unit.

[1]) Other gears used are, ring-net, pelagic trawl and fixed nets (pound-net). Their use at the present time is restricted to a few areas and seasons and too little is known of their relative efficiencies to be given detailed consideration here.

of the catches of drift-nets of known mesh size are compared with those taken with other types of gear.

The results from these investigations lead to two superficially conflicting conclusions.

(1) Changes in the length composition of the catch are brought about by relatively small changes in mesh size (Hodgson, Delsman).

(2) The mesh size actually adopted in the commercial fishery provides a reasonably representative sample of the exploitable stock in some areas (Bjerkan, Borley and Russell).

The results obtained by Borley and Russell suggest that the commercial nets used in the North Shields and East Anglian fisheries during the period covered by their investigations (1913—1914) exhibited relatively little mesh selection over the larger sizes. They conclude that the size distribution of the commercial drift-net catch is probably not determined to any great extent by the selective action of the net. Hodgson, on the other hand, concludes from his experiments that small changes in mesh size may bring about marked changes in the composition of the catch in these areas. He presents length measurements from drift-nets of three mesh sizes fished in these areas, which show changes in the length composition and in numbers caught with change in mesh size.

Bjerkan found that the length composition of drift-net and purse-seine and trawl catches taken in a number of localities were not substantially different and, like Borley and Russell, concludes that the drift-net provides reasonably representative samples of the North Sea herring stock.

It is evident from a review of these data that the apparent differences between the conclusions of the different authors can probably be attributed to the difference in size composition of the populations on which the experiments were performed, and to the range of mesh sizes employed. In Borley and Russell's experiments, the catches of the commercial drift-net fleets in use at the time were compared with trawl catches taken in the same areas, whereas in Hodgson's experiments the catches of specific nets, each of different mesh size and some of which had a considerably larger mesh size than the average for the commercial fleet as a whole, were compared.

Thus, the nets from which Borley and Russell's results were obtained were those chosen by the fishermen to catch the fish on the ground, whereas Hodgson's were selected from a fairly wide range of mesh sizes some of which were either much too small or too large for the fish population present on the grounds. Clearly, the extent of mesh selection by a drift-net of any mesh size will be governed by the overall size range of fish in the population; when this is narrow, escapes may only take place at one end of the range or not at all, but when it is wide, they may take place at both ends. The importance of stock composition in mesh selectivity is well illustrated by results of experiments with different mesh sizes in the Scottish fisheries off Shetland and off the east coast of Scotland, respectively. The herring population on the Shetland grounds has a narrower size range than on the more southerly grounds owing to the absence of substantial numbers of two and three-year-olds in this area. The bulk of the population lies between 25—30 cm. in length on the Shetland grounds and between 20—30 cm. on the east coast grounds. The results of mesh selection experiments conducted in the two areas from F.R.S. "Clupea" are given in Tables 1 and 2.

The Shetland data show much more consistent length composition and mean lengths over the range of mesh sizes used than do the north-east coast data, and they suggest that mesh selection is relatively small in the Shetland fishery. (Commercial nets in this fishery are mostly between 32—36 rows per yard). It is evident, on the other hand, that there is considerable rejection by the larger mesh sizes at the lower end of the size range in the north-east coast population (commercial nets are mostly between 33—36 rows per yard), but that rejection is probably relatively small above 24 cm. in length. Thus, while these data are too few for firm conclusions to be drawn regarding the acceptability of the commercial drift-net catch as the source of population data it

**Table 1. Percentage Length Composition of Catch—Shetland, June 1948.**

| Length (cm.) | Mesh size (rows per yard) | | | | |
|---|---|---|---|---|---|
| | 31—32 | 34—35 | 36 | 39—40 | 41—42 |
| 22 | — | — | - | — | — |
| 23 | — | — | — | — | – |
| 24 | — | — | — | — | — |
| 25 | 0·8 | 1·3 | — | — | 2·0 |
| 26 | 2·3 | 5·1 | 10·1 | 5·8 | 10·9 |
| 27 | 21·0 | 30·9 | 30·0 | 30·1 | 31·7 |
| 28 | 50·3 | 45·8 | 43·9 | 38·8 | 35·6 |
| 29 | 21·1 | 15·6 | 14·4 | 21·4 | 16·8 |
| 30 | 3·0 | 1·3 | 1·3 | 3·9 | 3·0 |
| 31 | 1·5 | — | — | — | — |
| 32 | — | · | - | — | · · |
| 33 | — | — | — | — | — |
| 34 | — | — | 0·3 | — | — |
| Mean length | 28·0 | 28·0 | 27·7 | 27·9 | 27·6 |

**Table 2. Percentage Length Composition of Catch—Scottish north-east Coast, June 1948.**

| Length (cm.) | Mesh size (rows per yard) | | | | |
|---|---|---|---|---|---|
| | 31—32 | 34—35 | 36 | 39—40 | 41—42 |
| 21 | — | — | — | 0·1 | — |
| 22 | — | — | — | 4·2 | 10·0 |
| 23 | — | 0·5 | 1·5 | 14·2 | 21·2 |
| 24 | — | 5·7 | 9·4 | 19·5 | 15·1 |
| 25 | 16·1 | 20·1 | 25·3 | 26·1 | 21·5 |
| 26 | 25·8 | 43·3 | 35·1 | 17·6 | 17·3 |
| 27 | 25·8 | 20·1 | 19·3 | 9·9 | 9·5 |
| 28 | 22·6 | 7·7 | 7·6 | 5·0 | 4·2 |
| 29 | 6·5 | 2·1 | 1·1 | 3·5 | 1·2 |
| 30 | 3·2 | 0·5 | 0·8 | — | — |
| Mean length | 26·9 | 26·1 | 25·9 | 25·1 | 24·7 |

would appear that mesh selection by the nets used in the commercial fisheries in these areas is not a serious source of bias in sampling the length composition of the autumn spawners over 24 cm. in length. Support for this tentative conclusion is obtained from the similarity between the mean lengths of the age-groups taken in the neighbouring trawl fisheries in late summer and autumn, which are known to exploit the same populations of fish.

**(ii) Other sources of drift-net selectivity.** Besides mesh selection, drift-net samples as normally obtained are liable to bias whenever the population exhibits depth stratification. The magnitude of this type of selection is very difficult to estimate, and its importance usually has to be gauged qualitatively. However, it is possible to obtain some assessment of the probable influence of this factor from known features of herring biology. The following may be listed:—

(a) The effect of physical discontinuity layers (e. g., thermocline) on diurnal vertical migration.

Temperature discontinuities, at least above some critical value, appear to act as barriers to the upward migration of herring at night. It is not known whether they are barriers to the whole population or part of it. There is evidence to suggest that they sometimes affect the vertical movements of herring in the northern North Sea in summer, and may result in unrepresentative sampling of the stock by some sections of the commercial fleet. However, it is considered that, while biasing the catch of some vessels from day to day, this factor will not give rise to large bias in the catch of a drifter fleet over a period of a week or a month (fishermen now recognize the importance of this factor and lower their nets accordingly). It will probably have greatest biasing effect on estimates of numbers in the population rather than of its length or age structure.

(b) Changes in behaviour with physiological state.

The characteristic diurnal vertical migration behaviour of herring on which the drift-net fishery depends, is most marked and regular during the non-spawning periods. At spawning, and for a time after spawning, this habit is probably much less regular, particularly amongst the older fish. At these times the drift-net fisheries will probably provide less representative catches of the ripe and newly spent fish. However, little is known of the degree of selection which takes place at these times and further experiments are needed to assess its importance.

(c) Differences in the powers of avoiding the nets within the population.

It is not known to what extent different sections of the population are able to avoid capture by drift-net through differences in "experience", sight, etc. Recent work in Germany (von Brandt, 1953) has shown that texture and colour play an important part in determining the catching power of the drift-net for some species of fish, but more detailed investigation is required for the North Sea herring.

A general assessment of all the existing data suggest that in those North Sea fisheries for autumn-spawning herring which are not centred on spawning and spent-herring populations, the drift-net catch provides samples of the length and age composition of the population exceeding two years of age which is reasonably unbiased. However, it is clear that many more data are required before any precise evaluation of the accuracy of the estimates can be made, and it is necessary that further comparative experiments be made in different parts of the North Sea, using drift-nets of different mesh sizes along with other methods of capture.

It is possible that the drift-net, as normally used, exhibits greatest selection at the spawning and immediate post-spawning season, but again more information is required before the bias due to this selection can be estimated.

**2. The herring trawl.**

The use of the herring trawl in the North Sea adult herring fisheries has grown enormously in the present century but as with the drift-net, relatively little is known about its sampling efficiency in different areas and seasons. Selection by the herring trawl will again be of two types, mesh selection, and selection due to its mode of operation in relation to the distribution of the population.

**(i) Mesh selection.** Unlike the drift-net, mesh selection by the herring trawl will operate above the lower section of the size range, the smallest sizes to be retained being mainly governed by the size of mesh in the different parts of the trawl. While for some roundfish species experiments have shown the cod-end to be the most important selection component in the otter-trawl, it is not known what part other net components play in herring trawl selection, although results published by Borley and Russell (1922) suggest that the baitings and belly may play a significant role. It is probable, therefore, that there may be differences in mesh selection between the many forms of herring trawl used in the North Sea fisheries due to differences in mesh size over the net as a whole. The effects of the rig, etc., or the shape of the meshes may also be important.

The only published data on selection by herring trawls fishing the adult populations were provided by Borley and Russell (1922) and Fulton (1922). Borley and Russell's results showed that there was little difference between the size compositions of the catches taken with trawls having cod-end, belly and baitings meshes ranging from 1·5 inches to 2·5 inches (stretched), and they concluded that practically no fish over 20 cm. in length escaped from meshes of these sizes. Fish as small as 15 cm. were caught in the nets with a cod-end mesh of 2 inches. Fulton presents data on the escapes of herring from cod-ends with mesh sizes of 1·25, 1·5, 1·75, and 2·0 inches, respectively. His experiments comprised covered-net hauls in two areas; in the Firth of Forth, where a young herring population between 8—22 cm. was encountered, and on the Dogger Bank, where the population was of larger fish, mostly over 20 cm. in length. Percentage

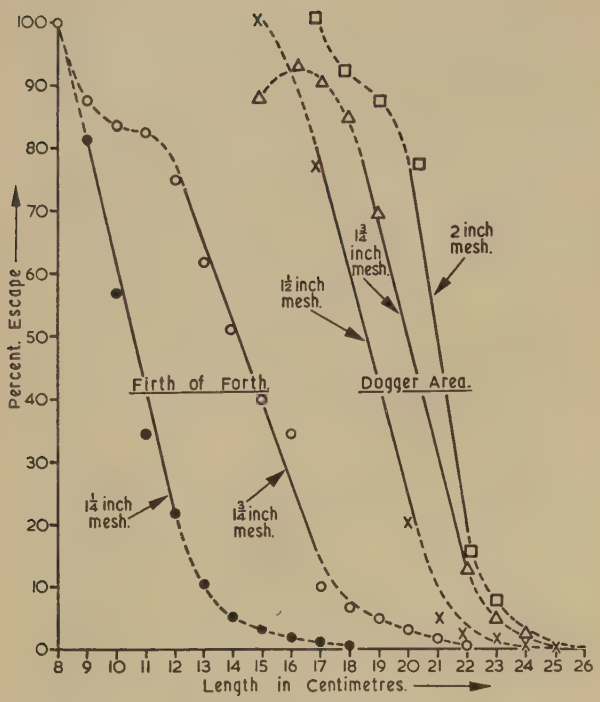



Figure 1. Cod-end mesh selection curves for herring trawl.

release curves drawn from his data are given in Figure 1. These results show a very marked difference in selection between the two areas. They strongly suggest that cod-end mesh selection of herring is very variable, depending on the stock composition and abundance. The Dogger results show, however, that escapes are very small over 22 cm. for all three mesh sizes, which agrees substantially with the conclusions drawn by Borley and Russell.

Although these data refer to experiments made with trawls which are now practically obsolete in the North Sea herring fisheries, it is probable that, for present-day herring trawls in which mesh sizes do not exceed 2·0 inches, there are very few escapes above 20 cm., but further experiments with modern gear are urgently needed.

**(ii) Other forms of trawl selection.** While mesh selection in the trawl may be less marked and complex than in the drift-net, selection due to other causes may be considerable. As with the drift-net, it will arise whenever the population exhibits depth stratification during the demersal phase of the diurnal rhythm; this may be different between areas, particularly when they are of different depths, and between physiological stages of the annual life-cycle of the fish. It is well known from echo-sounder surveys that herring shoals may be located at a wide range of depth from the sea-bed during daytime, especially in the deeper northern parts of the North Sea, and at some times and places part of or the whole population may be out of range of the trawl. Again, however, few published data are available from which to assess the biasing effect of this form of selection. Lucas (1936), on a re-examination of date published by Fulton (1922), found that the proportion of large herring caught by trawl at night was greater than by day, which he associated with differences between the vertical migration behaviour of the small and large herring. He suggested that there may be a continuous diurnal variation in the constitution of the trawl catches, from a stock containing a number of size groups. It is significant that the data on which these observations were made were taken at the immediate post-spawning periods in the northern and central regions of the North Sea, where the stock was composed of young immature and maturing fish and older ripe and spent fish. The difference in size composition between the day and night catches is probably due to differential diurnal behaviour between these two groups. This is supported by recent data taken by Skipper J. Main, of the Aberdeen steam trawler "Viking Honour", who kindly supplied the authors with records of the quantities and characteristics of herring caught by day and night during two herring trawling voyages to the Fladen Ground in October 1953. These data confirmed that the night catches contained a much higher proportion of older spent herring than the day catches.

It is probable that selection of size and maturity groups by the trawl varies seasonally and between areas which exhibit marked depth change. Selection is probably greatest in those fisheries based on adolescent and adult populations before the onset of spawning, and least during and immediately after the spawning season. At these latter times the trawl probably is a more efficient sampling gear, at least of the mature age-groups, than is the drift-net during the non-spawning phase.

In summary it may be tentatively concluded that while mesh selection does not seriously impair their efficiencies for sampling the North Sea adult stock, both the drift-net and the trawl may be highly selective over part of the size range of the stock, especially in some areas and seasons. The drift-net is probably more efficient than the trawl for sampling the non-spawning concentrations, but less so for sampling the spawning shoals. It is probable that trawl sampling during the spawning season provides the most representative length, age, and abundance data for the adult spawning stock in each area. However, other difficulties complicate its use at the spawning time for obtaining age census data in mortality calculations. These difficulties are discussed in a later section.

## Distribution of Sampling Effort in Area and Time.

It has been shown in Part I that one source of bias in sampled data is incomplete coverage of the area occupied by the population during the sampling period, particularly when the population exhibits stratification of one or more population variates. This is im-

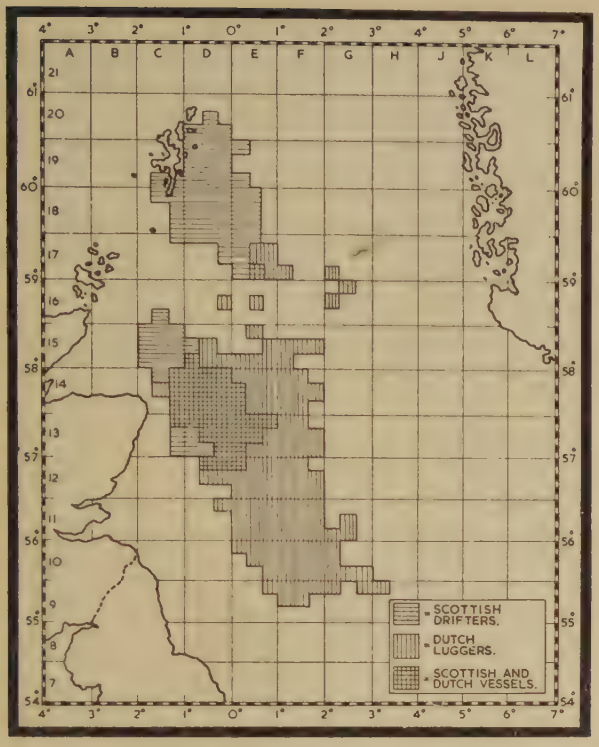



Figure 2. Distribution of fishing effort by Scottish and Dutch drift-net fleets in June 1952.

portant especially in those North Sea herring investigations which require sampling over wide areas within which a number of fisheries with different gears operate from different countries.

One example of these difficulties is provided by the summer drift-net herring fisheries in the north-western North Sea. Two main drift-net fisheries operate in this area, the Scottish and Dutch: the Scottish fleets fish daily from ports along the Scottish east coast and from the Shetlands, and exploit an area within a radius of 70—80 miles from the ports, so that sampling from their catches alone is limited to that part of the population to the west of about longitude 1° E. During the same period the Dutch fleet, which makes long voyages from the Netherlands, fishes mainly beyond the limits reached by the Scottish one; this is illustrated in Figure 2, which shows the area covered by the Dutch lugger and Scottish drifter fleets in June 1952 (for details see *Annales Biologiques*, Vol. IX, 1952).

Clearly, both the Scottish and the Dutch fleets failed to cover the whole range of distribution of the herring stock in the north-western North Sea in that month, so that biased estimates would be obtained of the length and age structure of the stock and of average abundance at that time, from samples taken from the Scottish or Dutch fisheries alone, if the stock were stratified as regards length, age or abundance. Our present knowledge shows that this is the case with each of these variates, and particularly with abundance, owing to the formation of local aggregations. These aggregations may change in position during the course of the fishing season and from year to year; indeed the success of the Scottish fishermen in May and June is partly governed by the extent to which the aggregations occur within the economic range of their vessels.

Comparable distribution problems arise in other parts of the North Sea, often of a more complex nature. The winter fishery in the eastern English Channel, for example, is pursued by a number of countries and a variety of gears, between which there is some degree of regional segregation, so that sampling from the catches taken by one country will not completely cover the whole population.

Two methods of overcoming these difficulties are possible:—

(1) By analysis of samples taken from all fisheries operating within the limits of distribution of the stock. (It is assumed that, in practice, the whole range of distribution at any time is covered by the combined fisheries of all countries).

(2) By the adoption of large-scale research vessel sampling using a standard gear.

Of these, (1) is considered the more practicable, particularly when the fishery is mainly with one type of gear, which samples the whole range of distribution of the stock. This is the case in the northern North Sea summer fishery, in the months May and June. It is less costly than (2) and permits more intensive sampling than is usually possible with the research vessel facilities normally available. However, it may be difficult in some areas where a multiplicity of gears are used, the comparability of which is not known. In these instances, research vessel sampling surveys may be the only way in which representative cover of the stock can be obtained. An assessment of the comparability of the gears used in such areas is urgently required because of the vastly greater cost of research vessel sampling.

A factor which must be borne in mind when the commercial fishery is used as a sampling unit, as in (1), is the non-random nature of the fleet distribution within the area fished, due to the aggregation of vessels in the most productive localities. This is particularly important in estimating indices of abundance for use in mortality calculations since the average values for periods within each year and between years will depend upon the variability of the aggregating properties of the stock and of the fishery. Herring populations exhibit marked changes in their degree of aggregation over short intervals of time and from year to year due to the influence of fluctuations in environmental factors, particularly during the non-spawning phase of the annual life-cycle. Therefore inaccurate estimates of mortality rates may result when they are calculated from average indices of abundance

of one or more year-classes obtained from sampling the commercial catch in two successive years.[1])

However, this difficulty can be overcome, if fishing effectively covers the whole range of distribution of the population, by estimating the index of abundance in each of a number of small sub-divisions of the area occupied by the stock, and using these to give an "aggregate index of abundance"[2]) for each area in each year. These indices are comparable from year to year whatever the change in aggregation properties of the fish stock and the fishery. (It is assumed that the sub-areas are small enough for the fishing effort in each to be regarded as effectively random, and for the average catch in each time interval to be independent of the amount of fishing).

**The collection of age-census data for estimation of mortality rates.**

One of the leading problems confronting European herring workers at the present time concerns the relationship between the amount of exploitation and the yield from the stock. This problem has become more urgent following the rapid post-war increase in exploitation of the adult stocks in the North Sea by trawlers, and the growth of fisheries for immature herring in some regions. While recent analyses of post-war commercial fishery statistics give no clear indication that fishing has yet passed the critical "over-exploitation" level, fishery trends in some areas confirm that a co-ordinated approach to the dynamics of the North Sea stock is urgently required.

Recent advances in the theory of fishing have provided the necessary theoretical equipment with which measures of the stock/fishing relationship for any species can be determined from known estimates of the four main population parameters, recruitment, growth, fishing mortality, and natural mortality. At the present time no determination of this relationship is possible for the North Sea autumn-spawning herring stock because reliable values for all of the population parameters cannot yet be calculated. In particular, age-census data are lacking from which the average mortality rate for the stock can be calculated.

The sampling programme to provide the necessary age-census data must, unfortunately, be designed in the light of a number of important unknowns in the biology of the herring stock. In particular, it is not yet known to what extent the autumn spawning herring population in the North Sea is divisible into discrete spawning communities, each with its spawning grounds and limits of distribution, or to what extent these communities mix during the non-spawning phase. Thus it is not possible at the present time to determine the limits of distribution of each community and so evaluate its population parameters separately, and determine the total amount of effort to which it is subjected throughout the year. It is possible, however, to attempt these evaluations for the autumn spawning stock as a whole, by ensuring that the sampling programme is conducted at times when these biological features are least likely to bias the age-census data. The most appropriate times are:—

(a) when the degree of intermixing is greatest, i. e., when the spawning communities are all or mainly contained within a common boundary.

(b) when the degree of segregation is greatest, i. e., when the boundaries of each community are most distinct.

In the North Sea these conditions are most nearly satisfied for the adult members of the stock during the summer feeding phase and the autumn and winter spawning phases respectively. It is probable that the adults (older than two years) of the autumn-spawning stock are contained within the northern and central regions of the North Sea during the months May and June, when they are fished over a wide area by drift-net and trawl by a number of European countries, but thereafter a gradual segregation into spawning concentrations takes place, and fishing becomes much more localized.

It is considered, therefore, that the most appropriate periods in which to obtain the age-census data for mortality calculations are May—June over the whole area fished by the European fleets, and at each spawning season. It is difficult from present knowledge to assess which of these two possiblities would provide the most accurate data; both have their merits and demerits. The chief merits of May—June sampling are:—

(1) The herring stock is contained within approximately continuous and reasonably well defined boundaries, as judged by the available commercial statistics, within which it is intensively fished. This permits the use of the commercial fleets as the sampling units.

(2) The whole area fished in this period is sampled by one type of gear, i. e., drift-net.

(3) The stock in this area at this time comprises all of the previously spawned age-groups and probably the greater part of the stock of recruit spawners.

The chief demerit of sampling at this time is that the stock is widely spread and probably in active motion within its boundaries, which are variable from year to year.

These difficulties are smaller when sampling is confined to the spawning areas. At these times the limits of distribution within each area are smaller; most of the spawning fisheries are by trawl so that gear selectivity is probably a minimum, and separa-

[1]) Non-random distribution of fish in the sampling area also presents problems in the analysis of the sampled data. Some of the statistical techniques for analysing non-random trawl data are discussed in Barnes and Bagenal (1951), Taylor (1953), Gulland (Contribution No. 3), and Jones (Contribution No. 4).

[2]) This method was developed by Beverton and Holt in their theoretical studies of the dynamics of fish populations, and is described in detail in "On the Dynamics of Exploited Fish Populations." (In press). See also Contribution No. 8 by Beverton and Parrish.

tion of members of the adult autumn stock from other racial types (i. e., spring spawners) is most easily made. However, other difficulties arise at these times: not all of the spawning concentrations are fished commercially by trawl (e. g., the Scottish north-east coast), so that sampling from the commercial fisheries must be supplemented in these areas by research vessel sampling; fewer of the age-groups in the stock are present in representative numbers on the grounds (i. e., only the adult spawners are present in representative numbers), and we have yet to determine the sampling characteristics and relative efficiencies of the many different types of trawls used in these fisheries.

It is considered that in view of the importance of the required data, steps should be taken to carry out intensive sampling programmes at both of these seasons, and that these data be used in a preliminary assessment of the relative merits of each. It must be emphasized here that this programme of investigation will provide only average estimates of the parameters for all spawning communities within the autumn spawning stock, and will only permit the approximate evaluation of the average total mortality rate for the stock as a whole. Much more information on the composition of the stock is required before this relationship can be determined for individual regional fisheries.

The basic sampling requirements may be listed as follows:—

(1) The collection of age frequency data in each of as many sub-areas of the range of distribution of the stock as possible. In the May—June fishery this might have to be restricted to sampling within each statistical rectangle covered by the fishery, but in each spawning fishery sampling within smaller area sub-divisions might be possible.

(2) The provision of statistics of catch and effective effort for the smallest practicable area and time sub-divisions of the fishing grounds (for further details see paper by Beverton and Parrish No. 8).

These demands can only be satisfied through international co-operation in the execution of the sampling programme, by pooling the age-frequency data obtained from each region and by the compilation of total catch and effort statistics on a regional basis for each drift-net and trawl fishery in the North Sea, at least for the periods in question. It is important that a sampling programme executed in this way would also provide data suitable for the evaluation of the other population parameters and of a number of other important biological features of the North Sea stock.

## Conclusions.

It is clear from the preceding sections that: (1) Important information is lacking concerning the sampling characteristics of gears used in the North Sea herring fisheries. (2) The nature of the fisheries may prevent the scientists of any one country from accumulating the data necessary for solving the fishing equation even approximately, so that (3) effective international co-operation in sampling the North Sea stock and pooling of basic data is urgently required. In particular, more precise information is required of the sampling efficiencies of drift-nets and herring trawls in each fishery. It is therefore recommended that selection experiments be conducted in as many areas as possible with both types of gear. Meanwhile, it is also recommended that steps be taken to effect international co-operation in sampling from the North Sea drift-net fisheries in May and June and the trawl fisheries on each spawning ground as well as in the compilation of catch and effort statistics on a regional basis.

8.

# Commercial Statistics in Fish Population Studies.

*By* R. J. H. Beverton *and* B. B. Parrish

The purpose of this paper is to discuss the rôle of commercial statistics of catch and effort in sampling projects and fish population studies in general, and to summarize, as far as is possible at the present time, the kind and quality of commercial statistics required for computing standardized measures of fishing effort and fishing intensity.

## 1. Introduction.

The process of catch sampling to obtain data for fish population studies can, for practical purposes, be considered in two stages. The first involves taking an individual sample and deducing from it the local abundance and structure of the population; this process might consist of making an experimental haul with a particular gear from a research vessel or of estimating the composition of a commercial vessel's catch by market sampling. The second stage is one of combining the information from a number of individual samples of either kind to obtain a comprehensive picture of the abundance and structure of the whole population.

It is in the second stage, and especially when estimating an index of total abundance, that adequate commercial statistics play an important if not an indispensable part, as is demonstrated by Gulland (Contribution No. 2). Going beyond the immediate problem of sampling to the interpretation of the resulting information and the use to which it is put, Beverton and Holt (Contribution No. 9) have demonstrated the importance of a knowledge of fishing effort in the estimation of mortality rates and, more especially, in the separation of total mortality into that due to fishing, and that due to natural causes. Finally, when the need arises to regulate a fishery, commercial statistics of catch and effort are again indispensable—not only for the efficient administration of the regulation but as an adjunct to biological data for testing whether a particular regulative measure is having the expected result.

These generalizations apply to every commercial fishery but with greater force as the size and complexity of the fish population and of the fleets fishing it increases. The North Sea herring illustrates this point as well as any. This stock appears to consist of several "spawning communities" whose degree of independence is still largely unknown, although considerable mixing between them certainly occurs at some seasons. The herring fleets of the various countries concentrate on one or more of the communities at certain places and times using, in all, a wide variety of gears. This complexity makes a study of the population dynamics of North Sea herring a difficult task; and it is becoming clear that any real progress in assessing the stock of herring and being able to detect the occurrence of overfishing must involve co-ordinated research among the nations concerned. But for these purposes mere pooling of sample data is not enough. Each gear, according to its selective properties, gives a somewhat different picture of the structure of that part of stock where it is used (see Parrish and McPherson, Contribution No. 7). Also the relation between density and catch per unit effort certainly differs greatly in some gears. The essential requirement is to obtain measures of the total abundance and structure of each independent spawning community, or of the stock as a whole, to estimate its mortality rates and to relate the fishing mortality to the total fishing intensity exerted on it. Commercial statistics of catch and effort of each country, broken down into suitable units of time and area, together with calibration factors to enable estimates of abundance and structure from various sources to be adjusted to comparable measures, provide the means of integrating herring research so that this objective can be reached. Without them, the information that it is possible to obtain by sampling the fish stocks is seriously limited and its interpretation, especially when complex problems such as overfishing are concerned, largely a matter of guesswork.

## 2. Definitions and theoretical considerations.

The main objective can be stated quite briefly. It is to obtain a measure of the total amount of fishing on a stock or subdivisions of that stock (e. g., races, size-groups or age-groups) in such units that when divided into the total catch it provides a true index of total abundance. This measure of fishing activity has been called the "effective overall fishing intensity" (BEVERTON and HOLT, in press) and denoted by the symbol $\tilde{f}$; if the total catch of a population or part of a population is $Y$, then its abundance, $N$, is given by the equation

$$N = \frac{Y}{c\tilde{f}} \qquad (1)$$

where $c$ is a constant. It is important to note that the same constant $c$ also relates $\tilde{f}$ to the instantaneous fishing mortality coefficient, $F$, generated by it and which would be estimated from catch samples of the same population; we have, in fact,

$$F = c\tilde{f} \qquad (2)$$

Thus the problem of obtaining an index of total abundance from commercial statistics of catch and effort is closely related to one of the most important uses to which the resulting data are put, namely the estimation of mortality rates: in both cases a knowledge of the effective overall fishing intensity plays an essential part.

We now consider the stages involved in computing an estimate of $\tilde{f}$ from commercial statistics of catch and effort, taking first the simple case of a stock fished by one method only. The two main factors are fishing power and fishing time, their product being fishing effort. For a given method of fishing and species of fish the *fishing power* of a vessel is defined, and measured in practice, in relative terms as the ratio of its catch per unit fishing time or per unit fishing operation (e. g., per hour's towing or per shot) to that of a vessel and gear selected as a standard and fishing on the same density of fish. Thus time does not enter as such into the definition of fishing power, and is in fact eliminated by measuring fishing power from the ratio of catches obtained over equal periods of time or in the same number of fishing operations. Two of the factors which govern the fishing power of a vessel, at least with some methods of fishing, are its size and that of the gear it can use; these two factors are usually, but not always, closely associated. For example, it will be shown below that gross tonnage is a good measure of fishing power for steam trawlers, but in some methods of fishing it may be better to define fishing power in terms of gear dimensions rather than vessel size. Calibration of fishing power in this way therefore enables all the vessels of a fleet to be allocated a fishing power factor, in the units appropriate to that method of fishing.

A unit of *fishing effort* for a vessel can be defined as the product of its fishing power, in the standard units for its type, and an appropriate unit measure of the time or extent that its fishing power is in operation. Again taking steam trawlers as an example, an "hour's fishing" is a suitable time unit, so that for this type of vessel a "ton-hour" is a standardized unit of effort. The fishing effort expended during a given period of time (e. g., a month or year) by a steam trawler could therefore be computed in standardized units by summing the product of its gross tonnage and the number of hours it had fished during that period.

It will be noted that fishing effort defined in this way is really an index of the chance that a fish in the area where the gear is operating will be caught during a given moment of time; in this sense, therefore, fishing effort is related to the effective volume of water (or area of sea-bed) swept by the gear in that time. As this depends to some extent on fish behaviour and can seldom be estimated with accuracy from gear dimensions and length of tow alone (although a rough estimate may be possible in some fisheries), it is not a convenient way of defining fishing effort for practical purposes. The spatial implication of the term fishing effort should, however, be borne in mind. Thus the need for standardizing units of fishing power and time is really a question of ensuring that the fishing activities of different vessels and gears can be expressed in units which refer to equal *effective* swept volumes, even though these are not computed as such.

The final stage is to relate standardized fishing effort to the fishing mortality coefficient it generates. For this it is necessary to compute the *fishing intensity*, defined as the concentration of effort in space, since the greater the fishing effort in a given area the greater is the chance that a fish present in that area will be caught. Account must also be taken of the extent to which high concentrations of effort occur where fish themselves are most concentrated, since the greater this tendency the greater will be the catch obtained by a given total effort, and hence the greater the fishing mortality generated in the stock as a whole. This problem is discussed more fully by BEVERTON and HOLT (in press) and GULLAND (No. 2); here it is sufficient to note that the essential requirement is to be able to compute effort for sub-areas and for time periods small enough for the density of fish in each to be regarded as constant with respect to space and time. Suppose that in the sub-area $i$, of size $a_i$, the total standardized fishing effort in a period of time $j$ is $g_{ij}$. Then the standardized fishing intensity in sub-area $i$ during period $j$ is

$$f_{ij} = \frac{g_{ij}}{a_i} \qquad (3)$$

The quantity $f_{ij}$ is, in fact, a true index, for the period $j$, of the chance that a fish in sub-area $i$ will be caught and is proportional to the fishing morta-

lity coefficient $F_{ij}$ in that sub-area and period, i. e., we have:—

$$F_{ij} = cf_{ij} \tag{4}$$

If the catch from sub-area $i$ in period $j$ is $Y_{ij}$, then the ratio $\frac{Y_{ij}}{f_{ij}}$ i. e., the catch per unit fishing intensity, is proportional to the average density $D_{ij}$ of fish in sub-area $i$ over period $j$, as defined by GULLAND (No. 2). Thus

$$\frac{Y_{ij}}{f_{ij}} = cD_{ij} \tag{5}$$

where $c$ is the same constant as appears in (4). The effective overall fishing intensity during the period $j$, $\tilde{f}_j$, is the sum of the intensities $f_{ij}$ in each sub-area weighted by the density of fish in each as estimated from (5). Thus, if there are $z$ sub-areas in all, we have

$$\tilde{f}_j = \frac{\sum_{i=1}^{z} f_{ij}\left(\frac{Y_{ij}}{f_{ij}}\right)}{\sum_{i=1}^{z} \frac{Y_{ij}}{f_{ij}}}$$

which reduces to

$$\tilde{f}_j = \frac{\sum_{i=1}^{z} Y_{ij}}{\sum_{i=1}^{z} \frac{Y_{ij}}{f_{ij}}} \tag{6}$$

It may be necessary to work with periods of time less than a year to avoid large changes in sub-area densities, in which case an annual value of $\tilde{f}$ is obtained by adding the values of $\tilde{f}_j$ over a year. The resultant estimate of $\tilde{f}$ is proportional to the annual fishing mortality coefficient estimated by random sampling of the catch, as defined by (2). It is important to note that to obtain a true value of $\tilde{f}$ from (6) it is necessary for estimates of catch per unit effort to be available from all sub-areas over which the fish population extends; obviously, if this is not so, it means that the abundance of part of the population is unknown. In this case the only procedure is to assume that the unfished part of the stock remains a constant fraction of the total stock; if this is valid a correct index of $\tilde{f}$ will be obtained by means of (6).

We have so far considered the case in which only one type of fishing method is used to exploit the stock. Where more than one method is employed it is necessary to express the amount of fishing by each in the same units before they can be combined, and the procedure depends primarily on whether the methods are such that it is possible to compare the catch per standardized unit of effort of each when fishing on the same density of fish. Suppose, for example, that the catch of a certain species obtained by a group of trawlers exerting a standardized effort $G_T$ is $Y_T$ and that vessels fishing the same density of fish but using a different fishing method (designated as $K$) exerted a standardized effort $G_K$ and obtained a catch $Y_K$. The two efforts $G_T$ and $G_K$ may be in quite different units of fishing power and time, but the ratio of the two catch per unit efforts provides the factor, ${}_TZ_K$, for expressing the effort by the gear $K$ in terms of trawler effort, i. e.:—

$$\frac{\frac{Y_K}{G_K}}{\frac{Y_T}{G_T}} = {}_TZ_K \tag{7}$$

The total standardized fishing effort on the stock in trawler units is therefore:—

$$G = G_T + {}_TZ_K \cdot G_K \tag{8}$$

and in this way it is possible to estimate a value of $\tilde{f}$ using the catch and effort of both methods.

Where no direct comparison of catch per unit effort by different methods is possible, the only procedure is to select one method as a standard reference, to compute an estimate of $\tilde{f}$ from the catch and effort of the fleets using it, and to multiply this by the ratio of the catch obtained by all methods to the catch by the standard method. In this case the efforts of the other methods are not used as such—because they cannot be expressed in comparable units—and the accuracy of the resulting estimate of $\tilde{f}$ depends solely on that for the fishing method used as reference. This should therefore be the one which gives the most reliable measure of overall intensity, choice depending on factors such as ease of obtaining reliable statistics of fishing power and time (in standardized units), extent of "coverage" of the stock in question, and freedom from complications such as "gear saturation" and "vessel interference" (see below).

### 3. Calibration of fishing power.

One method of calibrating the fishing powers of a fleet of vessels of the same type is to use a research vessel as a standard and fish it side by side with a number of commercial vessels covering as wide a range of size as possible. This has the advantage that the details of the gear used by the reference vessel are known precisely and can be kept constant, and that it is easy to ensure that it fishes as nearly as possible on the same density of fish as the vessel to be calibrated. The limitation is that despite all precautions catches are usually highly variable; it may therefore be impracticable to fish a research vessel against a sufficient number of commercial vessels to obtain a reliable index of their fishing powers. If, however, the time and position of the catches obtained by commercial vessels are known, this information can be used to calibrate a large number of vessels.

This is the method used by BEVERTON and HOLT (in press) to investigate relative fishing power in the

English *steam trawler* fleet working in the southern North Sea. British demersal statistics give the catch and position for each trip of each vessel, and by comparing catch per hour of vessels fishing at the same time and position a large number of estimates of fishing power were obtained relative to one particular vessel selected arbitrarily as a standard. Although the accuracy of any one of these estimates alone was not high, the combined results showed that relative fishing power was fairly closely proportional to gross tonnage, the relation being shown in Figure 1. Here the circles are the geometric means of the power factors of vessels comprising each 20-ton class from 80 to 240 gross tons, and the vertical lines indicate plus and minus twice the standard error of the mean. For large-scale routine standardization of commercial statistics on an international basis a simple proportional index of fishing power is desirable, and it is clear from Figure 1 that to take gross tonnage as proportional to fishing power would enable most of the differences in fishing power within the fleet to be accounted for. The fishing power of the smallest vessels (mainly drifter-trawlers) is, however, seen to be a little greater than would be expected from their tonnage alone; multiplying the tonnage of these vessels (up to about 130 gross tons) by a factor of about 1·2 would bring their fishing power-tonnage relationship into line with that for the rest of the fleet, and enable the simple gross ton to be retained as the basic unit with only slight extra complication.

This method of analysing commercial statistics of catch and effort has recently been extended by Gulland to other English steam trawler fisheries, including distant-water ones worked by vessels up to 720 gross tons. In every case he found a closely proportional relation between power factor and gross tonnage for all except the smallest vessels, as in the data of Figure 1. Gross tonnage has also been used by Hickling (1946) to calibrate the fishing "performances" of Milford Haven trawlers for hake, while Boerema (1950) showed that the fishing "capacities" of Dutch steam trawlers were related to nominal horse-power.[1]) The other approach, instead of using a vessel characteristic as an index of fishing power, is to determine an individual fishing power factor for each vessel, or group of similar vessels, in arbitrary units that depend only on the particular ship chosen as standard. This refinement may eventually prove worthwhile, but there is nothing in the results we have obtained so far to suggest that gross tonnage would not be an entirely satisfactory—and much simpler—index, provided the smallest vessels are assigned an extra factor.

[1]) Neither "performance" nor "capacity" is, however, the same as relative fishing power as defined here. The former is simply the average catch per 100 hours fishing of a vessel in a particular year, independent of ground; the latter is, like fishing power, a relative unit, and is measured by comparing the catch per day's absence of vessels fishing during the same month, but again without reference to position.

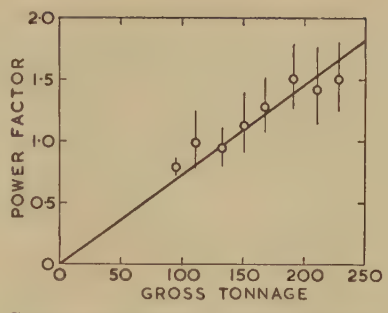



Figure 1. Gross tonnage as an index of fishing power for English North Sea steam trawlers. The circles show the geometric mean fishing power of vessels comprising each 20-ton class, and the vertical lines indicate plus and minus twice the S.E. of the corresponding mean. Data from Beverton and Holt (in press).

Beverton and Holt (ibid.) have also found that gross tonnage could be used as an index of fishing power for English North Sea motor trawlers,[2]) but with a different constant of proportionality. The average fishing power per ton of the motor trawler fleet was, in fact, found to be about 1·4 times greater than that of the steam trawler fleet, this being the factor needed to express motor trawler tonnage in terms of steam trawler tonnage to obtain comparable measures of fishing power. An alternative index of fishing power in motor trawlers was found to be brake-horse-power, two B.H.P. units being roughly equivalent in terms of fishing power to one M/T-ton, and hence to 1·4 S/T-ton. B.H.P. has also been used extensively by Gilis (e. g., 1953) to calibrate fishing power within the Belgian herring trawler fleet, though he does not appear to have published the actual relation between B.H.P. and fishing power. As horse power, rather than tonnage, is probably the more direct factor responsible for differences in fishing power between motor trawlers, it may be a better unit to adopt for general use. Thus if more powerful engines come to be used by the same-sized vessels, the B.H.P. would unit take account automatically of the increased fishing power of the fleet, whereas tonnage would not.

The fact that the larger of two trawlers has the greater fishing power may be partly due to the fact that it can tow the same-sized gear faster (or further per unit fishing time) than the smaller vessel but also because it may use a larger gear. Provided the relation between size of vessel and size of gear remains constant however, gear dimensions need not, for this purpose, enter into the index of fishing power. On the other hand, a gear modification increasing the efficiency of gear used by all vessels, including the reference vessel, would not alter relative fishing power within the fleet if tonnage alone is used as the unit. To make comparable estimates of fishing power before

[2]) Rounsefell (1948) states that the New England otter-trawl fleet (motor) is subdivided into three gross tonnage groups for estimation of fishing intensity.

and after the gear change, the increase in fishing power it causes must therefore be measured and incorporated in the fishing power index. For example, Bowman (1932) showed that the Vigneron-Dahl modification increased the fishing power of a trawl for haddock by a factor of about 1·4; hence the fishing power of a trawler of 100 tons would change from 100 to 140 units if it adopted the V.-D. gear. It is therefore essential that description of the gear in use should be recorded in sufficient detail to include any such permanent modifications affecting its fishing power. The other kind of gear characteristic that needs to be specified is selectivity; in trawls and seines this involves recording the size of mesh used—at least, that in the cod-end. The obvious effect of gear selectivity is to cause fishing power to vary with size of fish, but in addition there are indications that the size of mesh in towed gears may influence the fishing power on fish of all sizes, quite apart from mesh selection. This is presumably due, directly or indirectly, to the less resistance to tow offered by a large mesh than a small one, although the evidence is still not clear on this point. Nevertheless, a change in mesh size may require readjustment of fishing power indices by multiplying them by the increase in efficiency of gear with the new mesh to render them comparable, just as in the case of the V.-D. modification.

As far as we are aware, no detailed analysis of relative fishing power for other fishing methods has been published, but in most cases it is possible to deduce what might be a suitable index. From analysis of commercial statistics for *demersal seiners* landing mainly plaice in English ports, based on the method described above for trawlers, Gulland has found that differences in fishing power are unrelated to vessel size, at least, over the range 20—50 gross tons. This is presumably because over this range of size of vessel the size of gear used is the same, and power of vessel does not appear to be an important factor, at least in this class of seining. Provisionally, therefore, a unit of fishing power for English seiners is simply "1-seiner", but analysis of seiner fleets of other nationalities and working on other species may show fishing power to be correlated with some characteristic of vessel or gear. Silliman and Clark (1945) give data for the Californian *purse-seine* fishery for sardine which show that the length of net fished is related to size of vessel and so presumably is fishing power also, although the authors do not show this directly.[1]) Schaefer (1953), however, states that fishing power is related to vessel size in the tuna purse-seine fleet. In *drift-net* fisheries the length of "fleet", i. e., the number of nets shot, would seem to be the best measure of fishing power, and this information is recorded in the Scottish statistics for each landing of each vessel. Depth of net may also have to be taken into account in both purse-seine and ring-net fisheries, if it should be a variable factor. Similarly, in *long-lines*, the number of hooks (or multiple of it) fished by a vessel is an appropriate index of its fishing power, and a unit of this kind (the "skate", a length of line to which are attached about 140 hooks) is used in the Pacific halibut fishery. Thus Thompson, Dunlop, and Bell (1931) have shown that the catch obtained with a line having hooks attached at a constant distance apart is almost exactly proportional to its length, and hence to the number of hooks. With *trailed lines* (e. g., trolling) the number of lines operated by a boat presumably determines its fishing power, but the number of lines may be closely correlated with size of vessel, in which case a measure of vessel size may be an equally satisfactory and more convenient index of fishing power. Thus Schaefer (1953) states that catch per day of tuna fishing is related to vessel size in the American clipper fleet, thus being deduced from an analysis of commercial statistics as described above for trawlers.

Before leaving the question of fishing power, mention must be made of the problem of *gear saturation*. By this is meant any tendency for the fishing power of a unit of gear to vary with the amount of fish caught. Gear saturation is unlikely to be appreciable in demersal trawls or seines unless catches are extraordinarily heavy, but the fishing power of a drift-net or long-line depends directly on the number of vacant meshes or hooks; in theory, it begins to decrease from the moment the first fish is caught. The catch per unit effort of a gear liable to saturation therefore reflects correctly the direction of changes in abundance, but progressively underestimates their magnitude as the level of abundance increases; in other words, it makes abundance appear less variable than it really is. Little seems to be known about the extent to which gear does actually become saturated in commercial fisheries. No line fishery appears to have been examined from this point of view, but pronounced gear saturation has been demonstrated by Kennedy (1951) for the gill-net fishery of Great Slave Lake. He showed that the catch obtained was not proportional to the length of time the net had been in the water but followed a curve bending over to an asymptotic limit —at which limit the gear would be fully saturated and its fishing power nil. Some correction can be made for saturation if the saturation catch is known,[2]) since the fishing power of the gear when hauled is proportional to the ratio of the actual catch to the saturation catch. Gulland (in press) has shown that if it is assumed that fish encounter the gear continuously and uniformly along its length, the basic unit of fishing power for each haul of the gear in question must be multiplied by the quantity:—

[1]) The authors use a function of length of vessel and horsepower to define a unit of fishing effort for the California sardine fishery, but this is partly a measure of the greater speed and hence greater searching power of a large vessel than a small one. This latter problem is considered here in connection with defining appropriate units of fishing time.

[2]) This is not necessarily the catch that would be obtained if every mesh or hook was occupied by a fish, and would need to be determined experimentally (e. g., as described by Kennedy).

$$s \log_e \left( \frac{1}{1 - s} \right)$$

where $s$ is the ratio of the catch obtained in that haul to the saturation catch. A practical difficulty is that with shoaling fish a section of the gear may be fully saturated and the remaining part contain few if any fish; in this case the saturation catch is the greatest that could be taken by that part of the gear containing fish. Therefore, to adjust fishing power estimates for saturation it is necessary to know not only the catch obtained per haul of each unit of gear but also, if possible, something of the way in which the fish are distributed along the gear, as is recorded in Scottish herring statistics. Clearly, adjusting for gear saturation is not easy, and it has yet to be established that it occurs to any extent in North Sea fisheries; it may, for example, be important only at times of particularly heavy catches. Nevertheless, it would seem a matter worthy of investigation.

**4. Measures of fishing time: standard units of fishing effort.**

The appropriate unit of fishing time to take for various gears, by which a standardized unit of fishing power is multiplied to obtain a standardized unit of fishing effort, is less readily determined experimentally than fishing power and usually has to be deduced from a knowledge of the method of operation of the gear in question.

With most fishing methods, provided the process of catching fish is more or less continuous while the gear is being operated and not much time is spent in searching for fish without using the gear, a direct time measure of fishing activity is usually suitable. Thus in *trawling*, whether for demersal or pelagic fish and whether by bottom or mid-water trawl, the unit "hour's fishing" (or multiple of it) is appropriate. Thus a standardized unit of effort for steam trawlers is the "ton-hour", multiplied by any additional factors for gear efficiency that may be relevant. Similarly, in motor trawlers the "B.H.P.-hour" would be a standard unit of effort; because the time units are the same this effort unit for English motor trawlers would be multiplied by 1·4 to convert it to "steam trawler ton-hours" (see section 3).

The same time unit would also seem applicable to *seiners*, so that a unit of seiner effort would be a "seiner-hour". Comparison of catches of plaice by seiners and steam trawlers fishing at the same time and position (from English commercial statistics) has shown that 1 seiner-hour is equivalent, on plaice, to about 250 steam trawler ton-hours.[1]) The fact that a seiner may not fish at night nor for as many days per year as a trawler, is automatically taken into account by computing annual fishing effort from the total hours spent fishing during the year by each vessel.

Direct fishing time (i. e., hours fishing) may also be applicable to some *drift-net* and *long-line* fisheries; in others, "hours fishing" may not be a direct measure of the actual time during which fish are liable to capture. For example, in many drift-net fisheries for herring the fish "swim" for a much shorter time than the gear is fished in each operation. Here, a "net-haul" would be as good a unit of fishing effort as any, although if there should be any important and consistent differences in the duration of the "swim" between one area or season and another, it would be desirable to adjust net-haul units correspondingly. In the long-line fishery for Pacific halibut, Thompson, Dunlop, and Bell (1931) state that the length of time the gear is left to fish (the "soak") is effectively constant, and hence they use the "skate" as a standardized effort unit without introducing fishing time as such.

Although the use of a unit of operation instead of actual fishing time leads to more convenient effort-units, it is important to check that when fish are particularly scarce or abundant there is no tendency to change the duration of each unit operation. When fish are abundant during the East Anglian herring season, for example, the duration of each shot may be shortened; while at slack periods both the dusk and dawn swims are sometimes fished without lifting the nets. In this and similar fisheries, therefore, there may be a case for adopting a "net-hour" as a unit of effort rather than a "net haul". A further complication that may arise in drift-net fisheries is that fish are caught while the gear is being hauled. Since hauling time is very much influenced by the amount of fish in the net, it must be broadly correlated with the contemporary abundance of fish; consequently, it may be necessary to include in the effort unit a factor for hauling time. For example, taking the duration of the shot plus half the hauling time would probably result in an effort unit which would not be seriously biased by the abundance of fish.

Other instances of the bias that may be introduced by using a coarser measure of fishing time than the actual time the gear is in operation, is shown by considering the "day's absence from port", which is a time unit frequently used for trawl fisheries. It is simpler to record than "hour's fishing" and certainly easier to ascertain with accuracy, but it is linearly —not proportionally—related to true fishing time, the constant term being the time spent steaming to and from the fishing grounds. Thus "day's absence" is not a true measure of fishing time for comparing, for example, the fishing efforts of two fleets fishing the same stock but based on ports at different distances from the fishing grounds, though within either fleet it will give a true picture of changes in effort resulting from changes in fleet size. A more serious drawback is that the contemporary abundance of fish may alter

[1]) This figure is smaller than that obtained by Margetts (1949) from a comparative fishing experiment, but individual trawler/seiner comparisons are highly variable and the two estimates are not inconsistent.

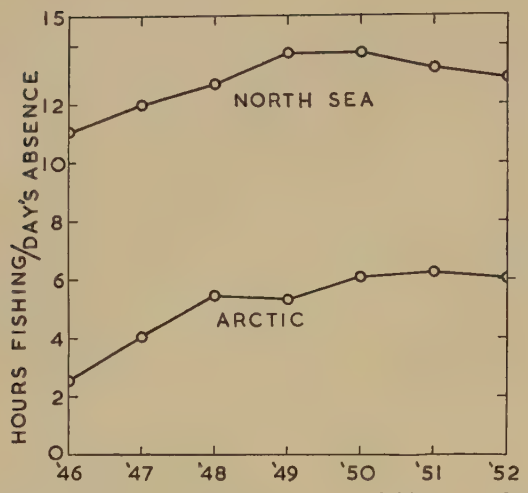



Figure 2. Trends in number of hours fishing per day's absence, 1946—52. The graphs show data for the English trawl fisheries in the North Sea and at Bear Island. The trend is ultimately due in each case to the declining abundance of fish during the period in question.

the relation between day's absence and actual fishing time within the same fleet. Examples of this are shown in Figure 2, where the hour's fishing per day's absence for English steam trawlers at Bear Island and in the North Sea are plotted for the post-war years 1946—1952. In each case there is an increase in the hour's fishing per day's absence, but it is much more marked for Bear Island where the change covers a nearly three-fold range. The change in the North Sea can be largely accounted for by an associated increase in the length of trip as the post-war abundance of fish declined, thus decreasing steaming time relative to fishing time, but for Bear Island the length of trip, if anything, decreased. Here the main cause is that the relatively great abundance of fish in the immediate post-war years resulted in ships having to lie to to clear decks for long periods before the gear could be shot again, thus decreasing the fishing time per day spent on the fishing grounds compared with later years. The conclusion from this is that wherever possible fishing time should be measured and recorded in commercial statistics as the actual time the gear is in operation.

We come, finally, to those fisheries in which vessels locate specific shoals of fish before shooting the gear and hence in which much time is spent searching with the gear inoperative. A notable example of this, in which the problem of computing a standardized unit of fishing effort has been discussed in some detail, is the *purse-seine* fishery for California sardine (SILLIMAN and CLARK, 1945). As well as similar types of fisheries such as *ring-net* fisheries for herring, some *trailed-line* fisheries and even possibly some trawl fisheries for pelagic species may fall into the same category. The important characteristic of these kinds of fisheries is that time spent searching (more exactly, the distance covered during the search) with the gear ready to use may have to be reckoned as part of the effort expended; it is, in fact, as if the gear itself had been used to search for fish but gave no catch until a shoal had been encountered. A knowledge of searching distance is therefore one essential for assessing "fishing time", and this must be distinguished in records from distance steamed to and from the general area where fish shoals are present—which may vary greatly from one year to the next. Searching time is, in fact, the only measure of fishing activity used by SILLIMAN and CLARK, but this is not necessarily a satisfactory procedure in general. For example, in one year shoals may be relatively far apart and considerable searching time may be required before they can be located. In another the same total abundance of fish might be aggregated in similar sized shoals but with the shoals themselves rather closer together. Then the same, or probably a greater, catch would be obtained with less searching time, giving a perhaps considerably greater catch per unit searching time although the total abundance was the same; in this case the number of hauls might be a better index of fishery activity than searching time alone. If vessels exchange information by wireless concerning the whereabouts of fish, a complication is that some vessels may not search even within the fishing area, but steam direct to where a shoal has been located. In some fisheries a further complication may be that if the local concentration of vessels becomes too high they make the fish more difficult to catch, either by dispersing shoals or by driving them to depths at which the gear cannot be operated; in this event the true fishing effort of a vessel would tend to decrease as the number of vessels fishing near it increased. This "vessel interference" as it may be called is a difficult problem to investigate experimentally, but there are indications that it may be important in the Whitby ring-net (I. D. RICHARDSON, personal comm.) and Shields drift-net (CUSHING, 1953) fisheries for herring, for example.

It must be concluded, therefore, that no general statements can at present be made on appropriate measures of fishing time, nor hence of fishing effort, in fisheries where searching is important. To determine these, each fishery would need to be analysed from the point of view of the shoaling habits and movements of fish and the searching tactics adopted by the fishermen. It is clear, however, that solution of this problem is bound to require particularly detailed commercial statistics for each trip of each vessel, such as catch, time, and position of catch, time or distance steamed while searching independently, and number of hauls.

### 5. Calculation of fishing intensity: sub-division of area and time.

It is shown above that the need for breakdown of statistics of catch and effort into sub-divisions of area and time arises when estimating the effective overall

fishing intensity $\tilde{f}$, or when computing an index of total abundance. The purpose is to reduce as far as possible the effect of changes in density of fish in space and time, and this in part determines the units applicable to the various fisheries. The other factor is, of course, the accuracy with which fishing positions and times can be recorded, but to some extent these criteria go together. For demersal fish in the North Sea the statistical rectangle ($^1/_2°$ latitude by 1° longitude, or roughly $30 \times 30$ nautical miles) certainly enables the grosser effects of non-uniform fish density to be eliminated, while no great changes in the average density in a rectangle occur within a period of a month—which is a suitable time unit. For herring, on the other hand, both these units are too large, and British statistics are broken down for analysis into sub-areas of one-ninth of a statistical rectangle (approximately $10 \times 10$ miles) or even smaller, and time units of a day, week or fortnight, as required. Dutch and Scottish herring statistics are published in sub-area units of $^1/_9$ of a statistical rectangle (Ann. Biol., Vols. VII—IX). This is possible for herring fisheries because the position and time of each catch can be recorded accurately on commercial returns; a sub-division as fine as this would be neither practicable nor so necessary in demersal fisheries. At the other extreme it may be noted that the sub-area unit adopted for the widely dispersed Pacific tuna fishery is in the order of $60 \times 60$ miles (Schaefer, 1953).

### 6. Estimation of total fishing effort by sampling.

A conclusion from the foregoing is that in every type of fishery the basic unit of commercial statistics should, if possible, be the individual record of each trip of each vessel. Not only is this necessary for computing effective overall fishing intensity and hence indices of total abundance, but the same information provides the best means of calibrating fishing power within a fleet and of standardizing fishing effort units for different fishing methods.

The "trip record" is the basic unit in British trawl statistics, and the concentration of the British trawling industry in a relatively few major ports makes it possible to obtain a complete census of every landing of every first-class vessel. This is, of course, the ideal, and collecting detailed information from every landing may be impracticable in a more dispersed fishing industry. In such a case a properly designed method of sampling landings would almost certainly provide sufficiently accurate estimates of effort for research purposes, with but a fraction of the man-power needed to cover every landing. Sampling surveys are employed on a large scale in Japan, for example, for the collection of fisheries statistics of all kinds (Yamamoto, 1953).

A sampling method is most effective if the total catch and/or the total number of landings in each period is known; these can then be used as weighting factors to estimate the total effort and its distribution from that of the sampled effort. Gulland (in press) has analysed demersal landings at Lowestoft in this way, using data of landings on one day of each week, i. e., sampling about $^1/_7$ of the total landings. He found that by raising the average effort (in standard units) of the sampled vessels for a month by the ratio of the total monthly catch to the sampled catch, the total monthly fishing effort could be estimated with a coefficient of variation of as little as 5 %. This procedure also gave a fair picture of the distribution of effort, especially in the heavily fished areas. If the total catch or total number of landings during the period is not known, the effort of the sampled vessels has to be raised by the ratio of the total number of landing days in the period to the number of sampled days. The accuracy of the resulting estimate of total effort now depends much on the day-to-day variation in the number of landings. At Lowestoft the number of daily landings may vary over a several-fold range during a week, with peak landings at the beginning and end, and the estimate of monthly effort by this second method is very much less accurate than by the first. It should be noted that raising by the ratio of the total number of days to the number of sampled days assumes that the number of landings per day on the sampled days is an unbiased estimate of the average number of landings per day during the whole period. With this method it is therefore very important that the sampling pattern should not coincide with any systematic weekly or monthly trend in the number of landings per day. This cause of bias does not exist in the first method, where the sampled effort is raised by the ratio of the total catch or number of landings to the sampled catch or landings; here it is only necessary to assume that the sampled catch per unit efforts provide an unbiased estimate of the average catch per unit effort for the period in question. In a fishery where all or nearly all the fleet returns to port each day the daily landings will of course be nearly constant and the second method satisfactory.

### 7. Conclusion.

We have endeavoured to show in this paper how sampling for abundance, and the use of the information in fish population studies, is dependent on a knowledge of the total fishing effort in standardized units and its distribution in space and time. This applies particularly in an internationally fished area such as the North Sea, where no one country can obtain a full understanding of its fisheries unless standardized international effort statistics are available, however intensive a sampling programme it may undertake. Yet it is noteworthy that while published commercial statistics give the catch of each species with great accuracy, few give statistics of fishing effort and none give them in a form that can be used to compute the total fishing intensity on a species in standardized units. It is difficult to avoid the conclusion that many of the more pressing tasks confronting fishery research at the present time—and especially those concerned

with stock assessment and fishery regulation—cannot be tackled really effectively unless the collection, standardization and dissemination of commercial statistics is greatly improved.

We have suggested that a remedy would be to abandon, where necessary, the conventional idea of fisheries statistics as complete censuses, and to work instead with estimates obtained by sampling. But even in favourable circumstances, where the basic data of catch, position and fishing time can be collected for every landing, it is still most unlikely that much of the other information needed for standardizing the raw effort statistics could be collected in this way—nor, indeed, would it be necessary to attempt to do so. Nearly all this additional information could be obtained well enough by sampling the landings, with a frequency depending on the variability of the factor in question within the fleet and on the rapidity of its change with time; or even, in some instances, by means of special surveys and investigations at relatively infrequent intervals.

Meanwhile, the first step would seem to be to establish standard international units of fishing power, effort and intensity for the major fisheries, so that the best use can be made of existing commercial statistics.

This is essentially a matter to be worked out between the countries concerned in each fishery, using in the first instance the information already available from either commercial statistics or comparative fishing experiments.

## Summary.

1. The role of commercial statistics of catch and effort in sampling projects and population studies in general is discussed.

2. The terms fishing power, fishing effort and fishing intensity are defined. It is shown how these factors can be combined to compute the effective overall fishing intensity on a species; this is proportional to the fishing mortality coefficient as estimated from catch samples, and when divided into the total catch gives a true measure of the abundance of that species.

3. Standard units of fishing power and fishing time, and hence fishing effort, are proposed for various fishing methods. Methods of correcting for certain complicating factors, such as gear saturation, are discussed. Standardization of effort units is most difficult in fisheries where much time is spent in searching for fish, notably in purse-seine and ring-net fisheries for pelagic species; in these instances special investigations may be required.

4. Appropriate sub-divisions of area and time are considered for computing effective overall fishing intensity in demersal and pelagic fisheries.

5. Estimating fishing effort and its distribution by sampling a small fraction of the total landings is proposed as worthy of consideration where collection of full effort statistics is impracticable.

6. It is suggested that the task of establishing international units of fishing power and effort in the major international fisheries should be undertaken as soon as possible.

# 9.

# A Review of Methods for Estimating Mortality Rates in Exploited Fish Populations, with Special Reference to Sources of Bias in Catch Sampling.

*By* R. J. H. Beverton *and* S. J. Holt

## 1. Introduction.

The use of catch samples for studying a fish population depends on the validity and accuracy with which characteristics of the population can be deduced from those of the samples. Of the factors which can be investigated and measured in this way, that which usually presents the most difficulty is mortality, partly because mortality rates are derived rather than simple quantities that can be sampled directly. They have to be estimated with the help of theoretical models of the population based on certain assumptions; these assumptions have themselves to be tested by observation or experiment before the mortality estimates derived from them can be accepted as reliable. Moreover, variability and, especially, bias in sample data can affect the accuracy of mortality estimates in complex and sometimes unexpected ways. In general, the estimation of mortality parameters makes a greater demand on the sampled data, with regard to both their extent and reliability, than does the analysis of any other factor; and it is probably true to say that if an adequate sampling system can be devised for this purpose it will almost certainly provide satisfactory measures of other parameters. It is for this reason that we have restricted the scope of this paper to a review of the ways in which sample data of various kinds can be used for estimating mortality rates.

A knowledge only of the age composition of a population enables us to find the total mortality rate, but separation of the two main components of mortality —that due to fishing and that due to natural causes— is more difficult. It can be achieved by observing the changes in age composition and abundance resulting from known changes in the intensity of fishing. In a fishery where the variation in fishing intensity (either from one year to the next through changes in fishing effort or with age of fish as a result of differential gear selectivity) is too small to produce a measurable change in age composition or is completely unknown, it is impossible to separate the mortality components using catch sample data alone, however extensive and reliable the sampling may be. In these circumstances it is necessary to turn to other methods involving the use of results from experiments of various kinds. These include tagging experiments, computation of the ratio of catch to total population size (e. g., as estimated from egg surveys), and assessment of the area "swept" by the fishing gear during a year. These methods can provide estimates of the fishing mortality alone, but if the total mortality is known from catch samples, natural mortality can be estimated by subtraction.[1]) Thus catch sampling is an essential part of any research programme aimed at estimating both fishing and natural mortality rates, and in this paper the main emphasis will be on the use of information obtained in that way.

Before proceeding, it may be helpful to recall the various causes of error in mortality estimates, the majority of which—though not all—are also responsible for variability or bias in the catch samples themselves. These causes can be grouped as follows:—

a) Those concerning properties of the fish population and habits of the fish; e. g., the effect of fluctuations in year-class strength on total abundance indices; tendencies for fish to segregate according to size or age; and dependence of the natural mortality rate on age, time, or population density.

b) Those involving characteristics of the fishing effort, e. g., changes in total effort or its distribution relative to the fish population.

[1]) Tagging experiments can, in theory, be used to estimate natural mortality directly, but only in rather favourable circumstances (see section 6(i)).

c) Those involving the characteristics of the commercial fishing gear and of the sampling device; e. g., gear selection (including release of small fish through the meshes and perhaps differential escapement of larger fish in other ways) and variation in sampling efficiency with fish density (e. g., through "saturation" of the gear by large catches).

d) Errors in age determination, in the case of methods based on age structure.

e) The basic statistical variation inherent in any sampling method. This is especially important where small samples are involved, as may be the case in research vessel sampling (as opposed to commercial catch sampling).

In every method of estimating mortality there will be errors from one or more of these sources; their relative importance will vary from one fishery to another. We shall be concerned primarily with sensitivity to bias from the first three of the above causes of error, discussion of (d) and (e) being more appropriate to a statistical treatment of the sampling system itself (see Gulland, Contribution No. 2).

## 2. Definition and Theoretical Treatment of Mortality.

It is convenient to distinguish two main kinds of mortality: that due to fishing, and that due to all other causes of death—the "natural" mortality. In effect, three ways of representing these have been proposed at various times:—

**(a) The annual expectation of death** (e. g., Baranov, 1918; Ricker, 1948). This is the fraction of the fish present at the beginning of a year that will actually die during that year from all causes or from a specified cause. The fraction that will be caught, i. e., the annual expection of death by capture, has been called the "rate of exploitation".

**(b) The annual mortality rate** (Thompson and Herrington, 1930; Ricker, 1944). This is the fraction of the fish present at the beginning of a year that would die during that year from a given cause if no other causes were operative. The fraction that would be caught in these circumstances is called the "annual fishing rate".

**(c) The instantaneous mortality coefficient** (Baranov, 1918; Graham, 1935; Parrish and Jones, 1953; Beverton and Holt, in press; and others). This can be defined most simply as the relative rate of decrease at a given moment due to any specified cause $x$, i. e., $\left(\frac{dN}{dt}\right)_x \cdot \frac{1}{N}$, where $N$ is the total number of fish.

The last of these is, in general, the most suitable method of representing mortality, partly because of its mathematical simplicity but more so because of the direct relation between an instantaneous coefficient and the cause of death. The instantaneous fishing mortality coefficient $F$, for example, is directly proportional to the fishing intensity generating it, provided the latter is measured in the appropriate units (see Beverton and Parrish, Contribution No. 8). Moreover, this relation is independent of the magnitude of natural mortality; but that between fishing intensity and the rate of exploitation is not independent in this way and, indeed, cannot be stated unless the value of the natural mortality rate is already known, while the annual fishing rate has little meaning in reality if there is death from causes other than fishing. We shall show below that the proportional relationship existing between fishing intensity and the instantaneous fishing mortality coefficient $F$ is of the greatest importance in analysing total mortality into its two components. The following theory uses instantaneous mortality coefficients throughout, but the inter-relations are set out in Appendix A and have also been discussed by Ricker (1948) and Widrig (1954).

## 3. Estimation of the Total Mortality Coefficient (F + M) from Catch Samples, F and M Constant.

Let us consider a population of fish in which fishing mortality can be represented by an instantaneous coefficient $F$ and natural mortality by an instantaneous coefficient $M$, both being constant. From definition (c) above, it follows that the population is decreasing at an instantaneous rate $\frac{dN}{dt}$ where

$$\frac{dN}{dt} = -(F+M)\,N$$

If the total number of fish at time $t_0$ is $N_0$, the solution of this differential equation, giving the number surviving at any later time $t$, is

$$N_t = N_0 e^{-(F+M)(t-t_0)} \qquad (1)$$

By taking natural logarithms of both sides we find

$$\log_e(N_t) = \{\log_e(N_0) + (F+M)t_0\} - (F+M)t \qquad (2)$$

The two variables in this equation, $\log_e(N_t)$ and $t$, are linearly related, the term in large brackets being constant and the slope of the straight line being the numerical value of the total mortality coefficient $(F + M)$. The true number $N_t$ cannot, of course, be estimated directly by catch sampling, but exactly the same relationship holds if $N_t$ is replaced by a proportional index of abundance, e. g., catch per unit effort. It should not be overlooked, however, that in deriving (2) it is assumed that both $F$ and $M$ are constants and, in particular, do not vary with the age of the fish or the population density; hence it requires that fishing intensity is also constant. The assumption of constancy of $F$ is particularly critical, since if $F$ should vary with age of fish as a result of differential gear selectivity, the age composition of the catch is

no longer the same as that of the population (as it is when $F$ is constant). This problem is mentioned further in section 5.

**3 (i). Relative age or length compositions only.**

The simplest form of presentation of data is the *age-frequency diagram*, in which the relative number in each age-group is expressed as a percentage of the total number of fish in the sample. This was called by BARANOV (1918) a *catch curve*, and some examples of the form such curves can have are discussed by RICKER (1948). In a catch curve, the fish comprising the various *age*-groups are of different *year*-classes, so that to use it to estimate mortality the effect of fluctuations in year-class strength have to be eliminated as far as possible by combining catch curves for a number of years sufficient to average them out, although this procedure necessarily introduces a form of weighting which may not be the best and which is not reproducible from one set of data to another. Nevertheless, if fishing effort has been fairly stable over a period of years the average catch curve may be valuable in giving an estimate of at least the order of magnitude of the total mortality coefficient $(F + M)$ from the slope of the descending straight line fitted to the natural logarithms of the age frequencies. This linear property of log catch curves has been observed in a number of exploited fish populations (e. g., JENSEN, 1939; SILLIMAN, 1943).

Economy of sampling effort may be achieved by estimating the total mortality coefficient from certain "integral" properties of relative age compositions, of which a simple example is the average age of fish. To avoid complicating factors such as mesh selection that may influence the frequencies of the younger ages, the average age, $\bar{t}$, could be computed by starting from the youngest age, $t'$, that is fully represented in the catch samples. The equation for computing $(F + M)$ is then

$$(F + M) = \frac{1}{\bar{t} - t'} \qquad (3)$$

(See Appendix B for derivation). This principle of "integral estimates" has possibly a wide application; for example, TAUTI (1947) and KURITA (1948) have developed methods for estimating $(F + M)$ from a knowledge of the maximum age and the average age of fish in a sample of known size.

The use of length measurements combined with age determination in the form of age/length keys is well-known as a means of increasing sampling efficiency (see e. g., TANAKA, 1953, for a recent review, and GULLAND, No. 2). However, length structure alone may be useful when regular age determination is, for one reason or another, impracticable, provided some measure of the growth rate is obtainable by methods such as experimentation in tanks, tagging, or measuring the change with time in the position of a mode in a length distribution due to a particularly strong year-class (e. g., GRAHAM, 1934; MOORE, 1951). Since the right-hand limb of a length-frequency diagram is generated by the combined effect of total mortality and growth, it follows that if the growth rate is known, $(F + M)$ can be estimated.

EDSER (1908) was probably the first to notice that if the logarithms of a length-frequency diagram for plaice were plotted, the right-hand limb was approximately a straight line. This is due to the fact that growth in length of plaice over a limited range of age is also approximately linear, so that over this range length can be taken as a direct index of age. BARANOV (1918), by assuming a proportional increase of length with age, developed the theory for estimating total mortality from a length-frequency diagram, while SILLIMAN (1945) extended this treatment to enable $(F + M)$ to be estimated from the average weight of fish in catch samples. Both these methods, however, are liable to give distorted estimates because the growth equations used give an adequate fit over a limited range of age only; for general use an adequate theoretical representation of growth over the full range of age likely to be encountered in samples is required. That which the authors have found most suitable is the growth equation developed by VON BERTALANFFY (1938), namely

$$l_t = L_\infty \left(1 - e^{-K(t - t_0)}\right)$$

where $l_t$ is length at age $t$, and $L_\infty$, $K$ and $t_0$ are constants determined by fitting the equation to growth data, as described by BEVERTON and HOLT (in press)[1]). If $l'$ denotes the smallest length of fish that are fully represented in catch samples, and $\bar{l}$ the average length computed from $l'$ upwards, the equation analogous to (3) for estimating $(F + M)$ is

$$(F + M) = \frac{K(L_\infty - \bar{l})}{\bar{l} - l'} \qquad (4)$$

(See Appendix B for derivation). For example, estimates of $K$ and $L_\infty$ for North Sea plaice are 0·095 and 68·5 cm. respectively, while the average length of fish above 27 cm. in commercial catch samples taken at Lowestoft during the period 1932—38 was 31·2 cm. Inserting these values in (4) gives an estimate of $(F + M)$ of 0·84, to be compared with the value 0·83 obtained from age composition data for the same period (see Fig. 1).

The usefulness of this method depends partly on the pattern of growth among the age-groups in the catch, the best conditions being a rapid increase of length with age over the important range, with the minimum of overlap between the length distributions of adjacent age-groups. These requirements are met to a sufficient extent in species such as North Sea

[1]) See GRAHAM (1952) and BEVERTON (1953) for a brief account of the incorporation of this equation in theoretical population models and its fit to growth data of North Sea plaice.

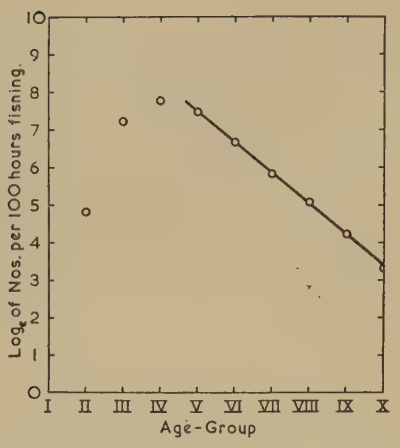



Figure 1. Age-composition of North Sea plaice. Natural logarithms of the average number of each age-group caught per 100 hours' fishing by Lowestoft steam trawlers, 1929—38. The slope of the line gives an estimate of the total mortality coefficient $(F + M) = 0{\cdot}83$.

plaice and cod; on the other hand, growth of North Sea herring above about four years of age is relatively slow. Here, the difference between $\bar{l}$ and $l'$ (on which the accuracy of the estimate of $(F + M)$ is critically dependent) would be particularly small and sensitive to factors such as sampling variation and fluctuations in year-class strength or growth rate.

### 3 (ii) Age composition and indices of abundance.

If catch per unit effort data are available, and these are considered to give reliable estimates of abundance, the age composition of the population can be expressed by indices of abundance of fish in each age-group. This makes it possible to compare the abundance of the same year-class in successive years of life, and an estimate of $(F + M)$ can be obtained by sampling in two or more successive years. From the point of view of sampling efficiency the best estimate of the abundance of an age-group is usually obtained by sampling continuously throughout a year (or fishing season); and we show in Appendix C that provided $F$ and $M$ are constant the mean annual estimate can be treated for mortality estimation in the same way as the instantaneous abundance $N_t$ postulated in (1).

Let us suppose that an index of the annual mean abundance of a year-class when in age-group $v$ (as estimated from data of catch per unit effort) is $\bar{N}'_v$, and $\bar{N}'_{v+1}$ when in age-group $v + 1$. Provided both age-groups are sampled with equal efficiency these indices are each related to the true abundances $\bar{N}_v$ and $\bar{N}_{v+1}$ by the same factor, i. e., we can write

$$\bar{N}'_v = k\bar{N}_v$$

and

$$\bar{N}'_{v+1} = k\bar{N}_{v+1}$$

in which $k$ is the constant of proportionality. From (1) we therefore have

$$\bar{N}'_{v+1} = \bar{N}'_v e^{-(F+M)}$$

and hence

$$\log_e\left(\frac{\bar{N}'_v}{\bar{N}'_{v+1}}\right) = (F + M) \qquad (5)$$

Ratios of abundances estimated over short periods (e. g., a month) whose mid-points are one year apart can also be used (JONES, Contribution No. 4), but this may involve difficulties due to variation in the seasonal pattern of abundance. If fishing effort has been reasonably stable over a period of years the abundance age compositions for each year can be averaged to eliminate year-class fluctuations as described above for age-frequency data, but with the advantage that the weighting procedure involved can be examined statistically. Figure 1 shows the average age composition of North Sea plaice for the years 1929—38 plotted as natural logarithms of catch per 100 hours fishing; the right-hand limb is closely linear and its slope gives the estimate $(F + M) = 0{\cdot}83$.

### 4. Separate Estimation of $F$ and $M$ from Catch Samples: $F$ varying with Time or Age.

In the preceding section we assumed both $F$ and $M$ to be constant; this enabled estimates of the total mortality coefficient $(F + M)$ to be obtained by sampling for age (or length) structure, but there was no way of analysing it further. To do this it is necessary in the first instance to assume $M$ to be constant, as before, and then to see how changes in fishing intensity are reflected in estimates of $(F + M)$. The more nearly proportional is the relation between intensity and total mortality the smaller $M$ must be, and *vice versa*. It will be seen that there are therefore two essential requirements for obtaining separate estimates of $F$ and $M$ from catch samples:—

a) There must be changes in fishing intensity —either with time on the stock as a whole (e. g., as a result of changes in total fishing effort or its spatial distribution, see below) or with age of fish (e. g., as a result of gear selectivity)—large enough to produce measurable changes in estimates of $(F + M)$.

b) The different fishing intensities must be known and expressed in standardized units so that they are proportional to the values of $F$ they generate (see section 2).

The required measure of fishing activity has been called by BEVERTON and HOLT (ibid.) the "effective overall fishing intensity" and denoted by the symbol $\tilde{f}$; it is computed from a knowledge of the spatial distribution of the commercial catch and effort as described by BEVERTON and PARRISH (No. 8) and GULLAND (No. 2). Since $\tilde{f}$ is proportional to $F$ we can write

$$F = c\tilde{f} \qquad (6)$$

where $c$ is a constant.

The basic equation for separating $F$ and $M$ can now be derived by substituting for $F$ from (6) in the total mortality coefficient, thus giving the equation

$$(F + M) = c\tilde{f} + M \qquad (7)$$

Hence $(F + M)$ is linearly related to $\tilde{f}$, the constant term being $M$. The procedure for estimating the two unknown parameters of (7), $c$ and $M$, and thus separating total mortality into its components, now depends on the circumstances responsible for the changes in $F$ that have occurred.

### 4 (i). Fishing effort stabilized at two different levels.

The essentials of this method were first developed by Silliman (1943) for the California sardine fishery. Here, the fishing intensity had been roughly stable for two periods each long enough for the corresponding total mortality coefficients to be estimated from catch samples as described in section 3 (i). From analysis of commercial statistics it was found that the fishing effort in the second period was about four times that in the first. Denoting parameters for the first period by the suffix $_A$ and for the second by the suffix $_B$, we have for the first period, from (7)

$$(F + M)_A = c\tilde{f}_A + M$$

and for the second

$$(F + M)_B = 4\,c\tilde{f}_A + M$$

Solving simultaneously gives

$$M = \frac{1}{3}\{4\,(F + M)_A - (F + M)_B\} \qquad (8)$$

and

$$c\tilde{f}_A = F_A = \frac{1}{3}\{(F + M)_B - (F + M)_A\} \qquad (9)$$

The estimates given by Silliman were $(F + M)_A = 0{\cdot}518$ and $(F + M)_B = 1{\cdot}612$, from which we find from (8) and (9), $M = 0{\cdot}15$, $F_A = 0{\cdot}36$ and $F_B = 1{\cdot}46$.

### 4 (ii). Fishing effort varying continuously with time.

This is the more general case in which the fishing effort on the stock as a whole varies from year to year during the period for which catch samples are available. As percentage age compositions cannot be averaged over a period of years in these circumstances, it is essential to work with age compositions expressed in indices of abundance so that the average abundance of a year-class in successive periods of life (usually years) can be compared. However, the log ratio of the annual mean abundance in a pair of years does not now provide, in itself, an estimate of the total mortality coefficient in either year (compare (5)). Instead, if an index of the mean abundance of a year-class in age-group $v$ in year $x$ is ${}_v\bar{N}'_x$, and ${}_{v+1}\bar{N}'_{x+1}$ in the following year $x + 1$ (when it is in age-group $v + 1$), (7) has to be written in the form

$$\log_e\left(\frac{{}_v\bar{N}'_x}{{}_{v+1}\bar{N}'_{x+1}}\right) + Q_{(10)} = c\tilde{f}_x + M \qquad (10)$$

where $Q_{(10)}$ is an additional term derived in full in Appendix D. The magnitude of $Q_{(10)}$ increases with the magnitude of the change in fishing intensity between each year of the pair, and it can be computed as described in that appendix. The principle of the method remains the same, however. In this case, given indices of abundance for two or more pairs of years and the corresponding annual fishing intensities, an estimate of the total mortality coefficient can be computed for each pair of years which is linearly related to the fishing intensity in the first year of each pair. Thus, plotting the left-hand side of (10) against $\tilde{f}_x$ should give a linear trend, the slope of the best fitting regression providing an estimate of $c$ and its intercept on the $y$-axis an estimate of $M$. If total mortality coefficients can be computed from monthly mean estimates of abundance one year apart, instead of annual mean estimates, they can be plotted directly against the value of $\tilde{f}$ for that year and estimates of $c$ and $M$ obtained without need for the term $Q_{(10)}$.

The number of sea fisheries for which estimates of age composition in indices of abundance have been published, and also in which fishing intensity is known and has varied sufficiently during the sampling period, is very limited. Thus although catch per unit effort data of this kind for North Sea plaice and haddock during the inter-war period are available, the variation in fishing intensity—as far as can be judged from the limited effort statistics available—was so slight that its effect on the estimates of $(F + M)$ cannot be distinguished from sampling variation. The method has, however, been applied successfully by the authors to Fry's (1949) data for the lake trout fishery of Lake Opeongo and to Rounsefell's (1949) data for the Frazer River salmon; in both these the fishing effort changed considerably. It will be noted that the larger the range of change in fishing intensity the lower need be the sampling accuracy of the abundance estimates to determine $M$ within specified limits, and *vice versa*. This use of catch sample data to obtain separate estimates of $F$ and $M$ therefore provides an objective criterion for sampling accuracy, and hence for the amount of sampling required in given circumstances. (See also Addendum, p. 83).

**4 (iii). Fishing intensity varying with age of fish.**

In the foregoing we have supposed that changes in $F$ are caused by changes in the total fishing effort, but the same principle can be used to separate $F$ and $M$ if $F$ changes in a known way with age of fish even though the total effort may be effectively constant. Such a change might be caused either by differential selectivity of the fishing gear for fish of various sizes or ages, or by the fleet tending to concentrate its activity—deliberately or otherwise—on some age-groups more than others. To develop the theory required it is convenient to suppose that differential gear selectivity is the operative factor; but in either case the age composition of the catch differs from that of the population, and to obtain comparable abundance indices the catch per unit effort of each age-group has to be adjusted to that of one particular age-group taken as reference.

Suppose, for example, that the youngest age-group, $v$, present representatively in the fishing area is taken as reference and that the fishing mortality coefficient for it is denoted by $F_v$; then that for any other age-group $v+r$ can be written as $y_{v+r} \cdot F_v$, where $y_{v+r}$ is the efficiency of gear on age-group $v+r$ relative to age-group $v$. The factor $y_{v+r}$ is also used to adjust the index of abundance for age-group $v+r$, i. e. $\overline{N}'_{v+r}$, obtained from the catch per unit effort of that age-group, so that it bears the same relation to true abundance as does the index for age-group $v$. Thus, if the true abundances of age-groups $v$ and $v+r$ are $\overline{N}_v$ and $\overline{N}_{v+r}$, and the unadjusted catch per unit efforts are $\overline{N}'_v$ and $\overline{N}'_{v+r}$, we have the relationships

$$\overline{N}'_v = k\overline{N}_v$$

and

$$\frac{\overline{N}'_{v+r}}{y_{v+r}} = k\overline{N}_{v+r}.$$

For any pair of age-groups $y+r$ and $v+r+1$, (7) therefore becomes

$$\log_e\left(\frac{y_{v+r+1} \cdot \overline{N}'_{v+r}}{y_{v+r} \cdot \overline{N}'_{v+r+1}}\right) + Q_{(11)} = y_{v+r} \cdot F_v + M \quad (11)$$

As in the case of (10), the log abundance ratio alone does not provide an estimate of the total mortality coefficient. The additional term $Q_{(11)}$ for (11) is given in full in Appendix D and solutions for $F_v$ and $M$ are obtained from a linear regression in a similar way, in this case by plotting the left hand side against $y_{v+r}$.

The main problem with this method is to obtain reliable estimates of the differential selection factors $y_{v+r}$, since on these depends the accuracy of the estimates of $F_v$ and $M$, as do those of $c$ and $M$ in (10) on the estimated change in fishing intensity. Where selection is due to escape through meshes, the selection factors can be estimated from the ratios of the catch of each age-group per unit fishing time of the commercial gear to that of a small-meshed gear fishing on the same population of fish, or on one having the same age composition, and preferably, density. In order to estimate $F_v$ and $M$ from (11) a minimum of three age-groups with differing selection factors are required; one of these could be the first that is completely beyond the mesh selection range, the other two lying partially or completely within it. If the mesh selection range is too narrow, or if entry to the catch is determined partially or wholly by recruitment of young fish to the fishing area (as in the British North Sea plaice fishery with the gear at present in use), the method cannot be used in this way. There is, however, the possibility that the catching power of the gear may differ among age-groups beyond the mesh selection range; if this can be measured it may be possible to use a number of age-groups and hence to obtain estimates of $M$ for a wide range of age. Comparative fishing experiments can also be used to measure differential selectivity of this kind, but only if it is possible to fish the same population as the commercial gear with a different gear which is known to catch all the age-groups in question with equal efficiency. The particular units in which the fishing effort of the calibrating gear is expressed need not, however, be the same as the commercial gear. Thus, suppose the catches per unit effort of age-groups $v$ and $v+r$ by the commercial gear are $Y_v$ and $Y_{v+r}$, while those of the calibrating gear are $Y'_v$ and $Y'_{v+r}$; the selection factor $y_{v+r}$, defining the ratio $\frac{F_{v+r}}{F_v}$ for the commercial gear, is given by the expression

$$y_{v+r} = \frac{\frac{Y_{v+r}}{Y_v}}{\frac{Y'_{v+r}}{Y'_v}}$$

whether or not the efforts of the two gears are measured in the same units (see also Beverton and Parrish, No. 8). An alternative method is to use marking experiments as described in section 6 (i), which avoids the difficulty of having to rely on one particular gear being truly unselective.

The above treatment of differential selectivity of a single gear can readily be extended to the case in which a population is fished by more than one type of gear, some or all of which differ in their selective properties. A notable example of this is the Lofoten cod fishery in which three different gears—the long-line, the gill-net and the purse-seine—have been in simultaneous use during recent years. Rollefsen (1953) has shown that the age compositions obtained from samples of catches by the three gears differ considerably throughout the age range; this must mean that the fishing mortality coefficient also changes with age. The extension of the above theory that is

required when more than one type of gear is operating can be shown most simply by supposing that only two gears, designated as $A$ and $B$, are involved.

Suppose gear $A$ is taken as reference, and that the fishing mortality coefficient generated by it on the youngest age-group, $v$, is ${}_AF_v$. With the previous terminology, the value of $F$ generated by gear $A$ on any higher age-group $v+r$ can be written as ${}_Ay_{v+r} \cdot {}_AF_v$, where ${}_Ay_{v+r}$ is the selection factor of gear $A$ for age-group $v+r$ relative to age-group $v$. The corresponding values of $F$ generated by gear $B$ on each age-group are obtained directly from the ratio of its annual catch of that age-group to that by gear $A$. Thus

$$\frac{{}_BF_{v+r}}{{}_AF_{v+r}} = \frac{{}_BY_{v+r}}{{}_AY_{v+r}}$$

The total fishing mortality coefficient generated by both gears in age-group $v+r$ can therefore be computed in terms of that generated by gear $A$ in age-group $v$ (i. e., ${}_AF_v$) by means of the expression

$$\begin{aligned} {}_AF_{v+r} + {}_BF_{v+r} &= {}_AF_v \left( {}_Ay_{v+r} + \frac{{}_BY_{v+r}}{{}_AY_{v+r}} \cdot {}_Ay_{v+r} \right) \\ &= {}_AF_v \cdot z_{v+r} \end{aligned}$$

where, for brevity, the factor $z_{v+r}$ replaces the expression in brackets. If indices of the mean annual abundance of a year-class in age-groups $v+r$ and $v+r+1$ are obtained in terms of the catch per unit effort of gear $A$, then (11) becomes

$$\log_e \left( \frac{{}_Ay_{v+r+1} \cdot {}_A\bar{N}'_{v+r}}{{}_Ay_{v+r} \cdot {}_A\bar{N}'_{v+r+1}} \right) + Q_{(12)} = z_{v+r} \cdot {}_AF_v + M \quad (12)$$

(See Appendix D for additional term $Q_{(12)}$). Provided the age selection factors for gear $A$ and the ratios of the catch of each age-group by the two gears are known, the factors $z_{v+r}$ can be computed and (12) contains only two unknown quantities, viz: ${}_AF_v$ and $M$, for which solutions can be obtained as before. The procedure for three or more gears operating together is a direct extension of this.

In the case of the Lofoten cod fishery Rollefsen states that there is probably no differential age selection with the purse-seine; if such a gear is taken as the reference gear $A$, then the selection factors ${}_Ay_{v+r}$ in (12) are all unity. A more important criterion in choosing the reference gear, however, is that its catch per unit effort should give the most reliable index of abundance for computing the log-ratio term of (12), and the purse-seine may not be the best for this purpose. Another feature of the Lofoten cod fishery, though one which might be present in any fishery based on spawning concentrations, is that fish enter the fishery by spawning-classes instead of year-classes, since all the individuals of a year-class do not mature at the same age (Rollefsen, 1935). In such a case it might be better to compute log-abundance ratios for a particular spawning-class in a pair of years, thus enabling all the data to be used, and to work throughout with spawning-classes instead of age-groups.

When differential fleet concentration on the various age-groups is the cause of the change of $F$ with age, the theory of the method is unchanged but the factors $y_{v+r}$ now refer to a property of the fleet instead of the gear. Provided the differential concentration is not too local and, at the same time, no large part of an age-group is completely outside the general fishing area, it should be possible to compute a value of $\tilde{f}$ for each age-group from age-composition data and a knowledge of the spatial distribution of catch and effort. The relative change in $\tilde{f}$ with age then provides estimates of the factors $y_{v+r}$. It may also be possible, in some circumstances, to use tagging experiments to measure this change of $F$ with age, as mentioned in section 6 (i).

It may be noted, finally, that (11) and (12) can be extended to take account of known changes in fishing intensity with time, as well as differential gear selectivity or fleet concentration, by writing $c_v \cdot \tilde{f}_x$ and ${}_Ac_v \cdot \tilde{f}_x$ in place of $F_v$ and ${}_AF_v$ respectively. The resulting estimates of $c_v$ and ${}_Ac_v$ then relate fishing intensity to fishing mortality for the age-group and gear (or fleet) in question.

### 4 (iv). The special case of $F$ = zero.

A special case of the above theory arises when $F$ is zero, the simplest of these being an unexploited stock when $F$ is permanently zero and natural death is the only component of mortality. In this case the methods of section 3 (i) for estimating total mortality give a direct estimate of $M$ (e. g., Ricker, 1949). It may also be possible to estimate $M$ in this way for young age-groups of an exploited stock that are below the retention range of the commercial gear, by research vessel sampling with a small-meshed gear.

Another possibility arises in a seasonal fishery where fishing is entirely restricted to a period less than a year's duration; in this case $F$ is temporarily zero during the closed season. If age-groups enter the fishery in the same time pattern each year it may be possible to estimate the abundance of a year-class at the end of one season and again at the beginning of the next, giving a direct estimate of $M$ during the closed season. Usually, however, seasonal fisheries are based on migratory species where age-groups may not enter with a sufficiently consistent time pattern each year to make this method reliable; for this reason and also to make best use of all the sample data, it may be better to estimate the average abundance of a year-class over the whole of each fishing season.

Finally, there is the possibility that $F$ may be zero temporarily for a period of a whole year or more, a notable example in the North Sea being the cessation

of fishing during the two world wars. If indices of abundance are available for one or more year-classes present in catch samples both just before and just after the war period, their log-ratios give a direct estimate of the average value of $M$ during the period. Application of this method to North Sea plaice (Beverton and Holt, ibid.) has given an estimate of $M$ of the order of 0·1. A less precise but more widely applicable use of war-time changes is that described by Beverton (unpublished report) and mentioned here for comparative purposes. The case considered is that of a fishery initially in a steady-state which is terminated by a sudden cessation of fishing for a known period. It is shown that the ratio of total abundance when fishing first starts again to the average pre-war abundance, or the ratio of the mean length of fish in pre- and post-war catch samples, can be used to specify a range of pairs of values of $F$ and $M$ within which the values for the pre-war period must have been. This information is of some value in itself, especially if the ratio is large since the possible range of $F$ and $M$ is then more restricted; but if an estimate of $(F + M)$ for the pre-war period is available, this, taken together with the war-time change, can give specific estimates of both $F$ and $M$. In a provisional application to North Sea plaice it is shown that war-time changes in both abundance and mean length, combined with the pre-war estimate of $(F + M) = 0{\cdot}83$ (see Fig. 1), confirm that $M$ is small. The special advantage of this method is that it may enable a separation of $F$ and $M$ without having regular age determination of catch samples or even—if the change in mean length is used—reliable indices of abundance.

A final point: It may seem at first sight that Silliman's method for separating $F$ and $M$ using two periods of stability (section 4 (i)) does not require indices of abundance either. It is, however, essential to know the relation between fishing mortality and fishing effort—which means also that age structure can be expressed in indices of abundance—and to know the relative change in fishing effort between the two periods. This information becomes unnecessary only when $F$ is zero in one period.

## 5. The Effect of Unknown Trends in $F$ or $M$ on Estimates of Mortality from Catch Samples.

The estimation of total mortality described in section 3 (i) assumes that both $F$ and $M$ are constant, while the methods for separating these coefficients mentioned in 4 (ii) and 4 (iii) depend critically on there being known changes in $F$ with time or age of fish, but it has still been necessary to assume that $M$ is constant. Estimates of $F$ and $M$ are likely to be biased if either have, in fact, a trend which is unsuspected, and these trends cannot always be measured, or even detected, from characteristics of the age structure alone.

### 5 (i). Trends in $F$.

The effect of a trend in $F$ on the age structure of a population is of course the same whether the trend is due to changes in total effort with time or to differential selectivity of age-groups by the fishing gear, but the age composition of the catch may be different in the two cases. With unknown changes in total effort, commercial catch sampling would nevertheless give comparable estimates of abundance from the catch per unit of each age-group—provided that the commercial gear is not differentially selective and that all age-groups are sampled equally by the fleet. But if the trend in $F$ is itself due to such selectivity, estimates of the abundance of each age-group by commercial catch sampling will be biased and the age composition of the catch will not be the same as that of the population.

Now the simple theory of mortality, with $F$ and $M$ assumed constant, leads to the prediction that logarithms of the catch per unit effort of a year-class when plotted against age should lie on a straight line. If one or more of the youngest age-groups are manifestly not on the straight line that fits the remaining points well, it is probably safe to conclude that these age-groups are not sampled representatively. This is known from other evidence to be the case with the first three points of Figure 1, for example, but the remainder are fitted very closely by a straight line. The question then arises whether this fact is, in itself, sufficient proof that $F$ (and, for that matter, $M$) is effectively constant over the range of age covered by the linear relationship, remembering that some scatter about the best fitting line is inevitable because of sampling variation and, probably, slight fluctuation in both parameters.

Figure 2 shows some hypothetical age compositions, in the form of indices of abundance of a year-class in five successive years of life, that result from certain postulated trends in $F$ with age; these are calculated from the theoretical models set out in Appendix E. For each trend we show:—

a) the age composition of the *population* (●), as would be obtained sampling with a non-selective gear,

b) the age composition of the *catch* (○) obtained by a differentially selective gear—or by a fleet that does not sample all age-groups equally—that is responsible for the trend in $F$ in the population.

A likely trend in $F$ is a steady *decrease* with age caused by fish becoming progressively more able to avoid capture as they grow larger. Figure 2 (a) shows the log age compositions of the population and catch, in arbitrary units of catch per unit effort, with $F$ decreasing arithmetically from 1·0 to 0·2 in steps of 0·2 each year as indicated on the $y$-axis, $M$ being constant at 0·1 throughout.

The log age composition of the population (●) is a definite curve, but that of the catch (○) is so close to the straight dotted line that in the absence of any other information it might seem reasonable to conclude that $F$ and $M$ were both constant (e. g., Jensen,

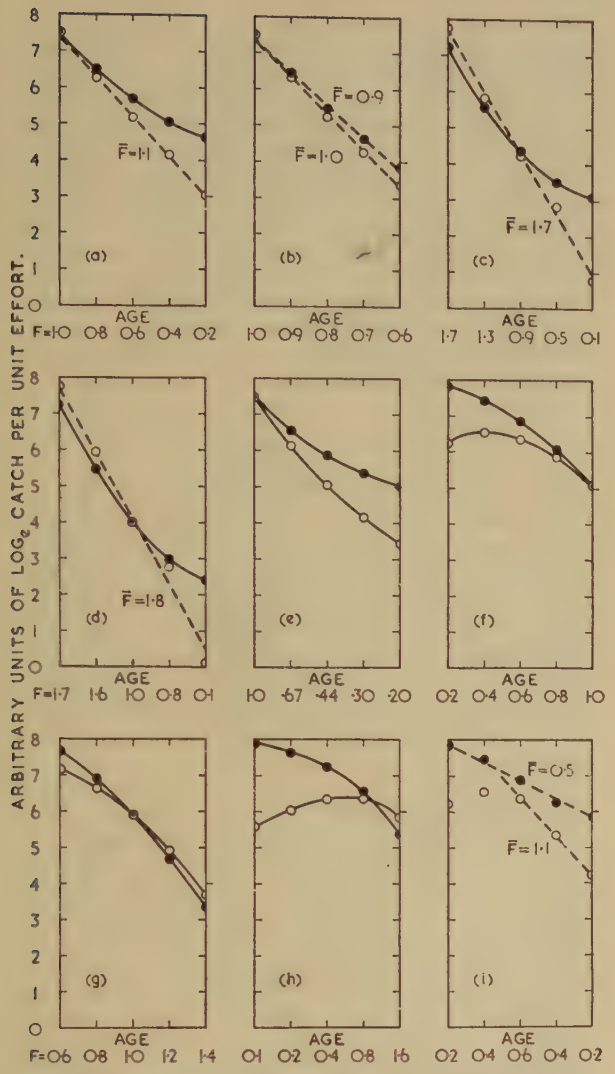



Figure 2. Trends in F with age. The solid points (●) show examples of population age-compositions (in log units) that result when the fishing mortality coefficient $F$ varies with age as shown below each diagram. The hollow points (○) show the corresponding catch age-compositions that would be obtained by sampling with the gear whose properties are responsible for the trend in $F$. The values of $\bar{F}$ shown in some diagrams are those that would be estimated from the slope of the lines if approximation to linearity is taken to imply constancy of $F$.

1939). However, the slope of this line is 1·2 which, with this interpretation, is the value that would be taken as an estimate of $(F + M)$; in fact, since $M$ is 0·1, this implies an apparently constant $F$ (which we denote as $\bar{F}$) of 1·1—higher than the actual $F$ for any age-group. What this means is that if $F$ were really constant at 1·1, the catch of each age-group would be almost identical to that actually obtained by the gear causing the decreasing $F$. Compared with a constant $\bar{F}$ of 1·1, the decreasing $F$ allows a progressively greater survival with increasing age, but if the same gear is used for catch sampling it progressively under-estimates the abundance at each age by almost the same amount. In Figure 2 (a) these two opposing tendencies nearly cancel out, so that the catches that would be obtained with the constant $\bar{F}$ and the decreasing $F$ are almost identical.

Figures 2 (b), (c) and (d) show three other examples of arithmetic decreases in $F$ with age. In 2 (b) the decrease (1·0 to 0·6) is less pronounced than in 2 (a), in 2 (c) it is decidedly severe (1·7 to 0·1), while 2 (d) shows the same overall decrease as 2 (c) but in irregular steps. In 2 (c) and (d) the age composition of the population shows fairly definite curvature, but the curvature might well not be regarded as significant in 2 (b). None of the catch age compositions show any well-defined curvature, but the extent to which the apparent constant $\bar{F}$'s differ from the actual trend will be seen from the values of $\bar{F}$ shown on the diagrams; in fact, the actual shape of a catch age composition with an arithmetic decrease in $F$ and a constant $M$ is sigmoid, but this would be virtually impossible to detect in practice. It is only when the decrease in $F$ is geometric (Figure 2 (e)), that the log age composition of the catch might be suspected of curvature.

Figures 2 (f), (g) and (h) show examples of $F$ *increasing* with age as indicated on the diagrams. In each case both the population and catch age compositions have fairly well defined curvature; in 2 (f) and (h), where the initial value of $F$ is small, the catch curves have a mode that would be clearly detectable in practice. Finally, 2 (i) shows the case of $F$ first ascending and then descending with age, as might occur for example in drift-net fisheries. Here the population age composition is virtually linear throughout, giving a value of $\bar{F}$ of 0·5, or just less than the highest actual value of $F$ (0·6). The abundance of age-groups in the catch, however, increases while $F$ is increasing but then decreases linearly. A not unreasonable interpretation in this case would be that the first two points indicate incompletely recruited age-groups or are influenced by mesh selection and should therefore be rejected, but that $F$ is constant for the last three age-groups. However, $\bar{F}$ estimated from the latter is 1·1, or nearly twice the highest actual value of $F$.

The conclusion from the examples shown in Figure 2 is therefore that there is a considerable range of trends in $F$ that could produce a catch age composition, and some that could produce a population age composition, indistinguishable in practice from that caused by a constant $\bar{F}$ having a value outside the actual range of the varying $F$. Particularly misleading are the age compositions given by a commercial gear that is progressively less efficient on fish of increasing age. The consequences of using an estimate of an apparently constant $\bar{F}$ for assessing the condition of a fish stock and, in particular, for predicting the effects

of certain regulative measures are not, however, necessarily as serious as might be thought. Provided the theoretical models used for these purposes are also based on the assumption that $F$ is constant, it seems that certain kinds of predictions, notably those of the effect of changes in total effort on steady yield, may not be seriously in error. The danger is, however, that attempts to break down an apparently constant total mortality coefficient when there is in fact an unknown trend in $F$ may lead to a serious error in the estimate of $M$. The whole question is evidently one that needs further investigation. Meanwhile, the insensitivity of sampled age compositions to certain major trends in $F$ would seem to call for every effort to be made to measure as accurately as possible any differential selectivity of commercial and, especially, sampling gear, either by direct comparative fishing experiments or tagging methods as described in 6 (i). It shows also the importance of a statistical analysis of the sampling system for establishing whether or not an observed age composition could have a significant trend.

### 5 (ii). Trends in $M$.

Provided the commercial and sampling gears are non-selective or their differential selectivity is known, trends in $M$ with age can be detected in age structures; otherwise, of course, it is virtually impossible to distinguish between trends in $F$ and $M$. For example, if $F$ is constant, an $M$ increasing with age will usually result in the log age composition curve bending downwards, while the reverse is true for an $M$ decreasing with age.

A more detailed analysis of trends in $M$ is complicated by the fact that the pattern of change in $M$ from one age to the next is seldom known *a priori*, as is the change in $F$ with age if effort statistics or gear selectivities are known. Consequently, the terms that need to be added to the left hand sides of (10), (11) and (12) cannot be computed directly, since they depend on the magnitude of $M$ in both years of the pair (see Appendix D). However, if $M$ does not change rapidly with age and is small relative to $F$ (as may well be the case in many heavily fished stocks), the additional term can be ignored and computing log-abundance ratios for successive pairs of age-groups could show a range of change of $M$ with age.

More serious may be the consequences of a trend in $M$ with either age or population density when applying the methods of section 4 for separating the components of total mortality. In the analysis of two stable periods (section 4 (i)) the different levels of fishing effort will cause both the average age of fish and the population density to be different in the two periods. If $M$ is correlated with either, it also will be different and this will lead to error in the estimates of $F$. Such trends are also likely to bias estimates obtained by the method of section 4 (ii), which utilizes changes in effort with time, if the log-abundance ratios are computed from all the age-groups in the exploited phase of the population. In this case the points at high efforts will tend to be associated with lower densities and average ages than points at low efforts, causing a rotation of the regression line. This could be largely avoided by computing log-abundance ratios for each pair of age-groups separately and fitting a separate regression to each, thus minimizing the effect of a trend in $M$ with age; while splitting the data into groups of roughly equal population density and fitting a regression to each, would enable any variation of $M$ with density to be assessed. However, if natural mortality is both large and variable, an analysis of the causes of death, enabling more realistic theoretical models to be set up, would be required for its proper estimation.

## 6. Methods of Estimating $F$ other than by Catch Sampling.

The preceding discussion has shown the requirements that must be met to obtain a reliable estimate of the total mortality coefficient ($F + M$) by catch sampling and, further, to distinguish its components. There are, however, three other methods of estimating mortality in exploited fish populations, namely by tagging experiments, by estimating in absolute units the abundance of the population and the total annual catch, and by considering the area "swept" by the fishing gear in a given period.

### 6 (i). Tagging experiments.

The idea here is that by setting up an experimental "sub-population" of tagged fish it may be possible to obtain more detailed and accurate information than from catch samples of the whole population. However, compared with the untagged population, the properties and problems of analysis of a tagged population may differ in a number of respects which are relevant to mortality estimation.

*Advantages.*

a) A known number of tagged fish are liberated at a known time and place; that is, recruitment to the sub-population is controlled.

b) If tagged fish can be identified on recapture, either as individuals or as members of particular batches, the period at liberty is accurately known and age determination is not required.

c) If the distribution of fishing effort is known sufficiently accurately it may be possible to select a liberation area in which the local fishing intensity changes much more rapidly than the total effort, thus enabling a division of total mortality into its components by methods analogous to those described in section 4.

*Possible complications.*

d) The actual number of tagged fish from which subsequent recaptures are obtained may be very different from the number liberated, through heavy

mortality—due to the tagging operation—within a short time of release. In this event use of the number liberated results in $F$ being underestimated (cf. e)).

e) There is unlikely to be complete detection and reporting of all recaptured fish; this has the same effect as d) in that use of the number liberated leads to $F$ being underestimated.

f) The operation of tagging or the presence of a tag may make a fish more or less liable to capture than an untagged fish. If the effect is temporary it is necessary to discard recaptures until the effect has disappeared, which again means that the number liberated is of no direct value. If the effect is permanent there seems to be no way of adjusting the value of $F$ for the tagged population to agree with that for the untagged population (except perhaps by special experimentation).

g) Unless tagged fish can be distributed rapidly throughout the whole population in numbers proportional to the population density, the $F$ obtained from recaptures will probably not be the true $F$ in the population because the tagged fish are unlikely to be subject to the same effective fishing intensity. Usually, tagging has to be restricted to a limited area, in which case the estimate of $F$ thus obtained has to be weighted by the distribution of commercial catch and effort to give the true $F$.

h) With a limited tagging and recapture area, dispersion of tagged fish from it appears as part of the "natural mortality" unless a direct estimate of the dispersion rate can be made.

i) Tags may become detached from living fish. This also appears as a component of "natural mortality", although it may be possible to estimate the rate of tag loss by subsidiary experiments.

j) Finally, the presence of a tag may itself be an additional cause of death among the tagged population, and there is no way of treating the data to distinguish this from the true natural mortality rate in the untagged population—except again, possibly, by taking account of tank experiments on viability.

The last three factors mean that the true natural mortality coefficient $M$ must be replaced, for the tagged population, by a composite "other loss" coefficient $X$. Only if the effect of tagging on the survival of fish can be reliably established from long-term tank experiments, and dispersion from the tagging area and loss of tags from living fish can be estimated separately (see Beverton and Holt, in press), is it possible to use tagging data to estimate the true $M$ for the whole population. To our knowledge, these requirements have never yet been met in any tagging experiments in a major sea fishery, although controlled marking experiments have been carried out in lakes (e. g., Shetter, 1952). On the other hand, it may be possible to obtain a reliable estimate of $F$ by separating it from the total loss coefficient $(F + X)$ in the tagged population using methods analogous to those mentioned previously. Thus the natural logarithm of the ratio of recaptures obtained in successive periods after liberation gives a direct estimate of $(F + X)$ provided the fishing effort is constant, while if factors d), e) and f) are not involved, the number liberated can be used to obtain a separate estimate of $F$ (see Appendix F). If the fishing effort after liberation changes in a known way, $F$ and $X$ can be separated by an exactly analogous method to that mentioned in section 4 (ii), for which only indices of abundance of tagged fish are required. The advantage here is that since the number liberated is not used, recaptures can be disregarded until a sufficient time has elapsed for any temporary effects of tagging to disappear and tagged and untagged fish to become well mixed. Moreover, as *ratios* of abundance are computed, the fact that not all recaptured fish may be detected or reported (factor e) above) does not effect estimates of $F$ or $X$ obtained in this way, provided the percentage reported remains reasonably constant.

It must therefore be concluded that the calculation of both $F$ and $M$ from tagging experiments alone makes as much and perhaps more demand on data than does their estimation from catch samples. On the other hand, it may be that a combination of tagging and catch sampling could provide information that would be unobtainable from either source alone. For example, it may be possible to obtain a reasonably good estimate of $F$ from tagging data which could give no useful information about the magnitude of $M$, while it may often be relatively easy to estimate the total mortality coefficient $(F + M)$ by catch sampling but quite impossible to analyse it further: $M$ is then obtained at once by subtraction. A still less exacting use of tagging data (in conjunction with catch sampling) is as a means of calculating the *relative* values of $F$ for a series of size- or age-groups when these vary because of either differential selectivity of the commercial gear or, possibly, differential fleet concentration; it may then be possible to apply the methods of section 4 (iii) to make a full analysis of mortality from the catch sample data.

The fact that the absolute values of $F$ are not now required has several implications for the design and analysis of the tagging experiment. When measuring differential gear selectivity, for example, there would be no need for tagged fish to be randomly distributed among the whole population; on the contrary, they could deliberately be concentrated where fishing is heaviest, thus making the recapture rate as high as possible. Apart from the obvious advantage of this from the point of view of experimental efficiency, the higher the recapture rate the shorter would be the time needed to obtain a statistically adequate number of recaptures, and the greater would be the tendency for the influence of other losses to be masked or avoided. Furthermore, by restricting comparison to fish tagged and liberated together, the effect of such complicating factors as remained would tend to be equalized between groups. If these requirements can be met sufficiently well, the relative values of $F$ (and hence the factors $y_{v+r}$ of (11)) are simply in the proportion of the percentage of recaptures obtained

from each group per unit time. An obvious precaution would be to use a type of tag that does not materially influence the chance of the fish being retained by the gear, e. g., by becoming entangled with the meshes or by hindering swimming; while to exclude the possibility of preselecting the most easily caught members of a size- or age-group—should such inherent differences in catchability exist—it would be preferable to catch fish for tagging with a non-selective gear or, at least, a gear other than the commercial one.

Measurement of differential fleet concentration by tagging is less straightforward, partly because tagged fish of each age must for this purpose be exposed to the same effective intensity of fishing as the untagged members of their age-group, and hence must be mixed with them as thoroughly as possible. If the mature fish aggregate in a relatively small area for spawning, it may be possible to achieve fairly complete and rapid mixing by tagging from the spawning concentration; but it may still be necessary to work with a recapture period of a full year to cover the annual cycle of fleet distribution, so that it is unlikely that the advantages of a high recapture rate and short recapture period could be utilised. For each group, $F$ would have to be separated from the "total loss" coefficient $(F + X)$ as in Appendix F, but with the advantage that certain of the factors directly responsible for bias in $F$ (e. g., d), e) and f)) are no longer a source of error unless the extent of the bias differs in the various age-groups. The same procedure is, of course, applicable to the measurement of differential gear selectivity if the simpler method outlined above could not be used.

The use of catch data as an adjunct to a tagging experiment is well known: thus the Lincoln Index method of estimating total numbers is based on a knowledge of the ratio of tagged to untagged fish in samples, while DELURY (1951) has shown how catch and effort data for tagged and untagged fish can be used to detect the influence on the tagging data of certain of the complicating factors listed above. The methods proposed here differ from these in that the main emphasis is on commercial catch sampling, the purpose of tagging being, in effect, to investigate the sampling properties of the fleet and the gear, and to increase the reliability of the catch sample data and the information obtainable from it.

### 6 (ii). Estimation of the ratio of catch to total stock.

It follows directly from the theory of mortality outlined in section 2 that $F$ is given by the ratio of the total annual catch to the annual mean fishable stock. The details of the method depend primarily on how the total stock is estimated. In relatively small enclosed areas (e. g., lakes) tagging can be employed, using PETERSEN's method or various well known elaborations of it (e. g., SCHAEFER, 1951), but unless tagged and untagged fish behave similarly the estimate of total population size is influenced by many of the complicating factors listed above. Changes in sex ratio through selective capture have been used to estimate the size of some populations of terrestrial animals (e. g., PETRIDES, 1949), and the method may be applicable to fish stocks. Probably the best method is from *egg surveys*. If the seasonal egg production can be estimated, then a knowledge of the fecundity of mature females of different sizes will give an estimate of the total stock weight of mature female fish. In this case the catch must be sampled for sex ratio and maturity of females in order to compute the annual catch of mature females, but it is unnecessary to convert weight to numbers provided the egg production of an individual fish is proportional to its weight. This is true of North Sea plaice, in which a rough estimate of $F$ can be obtained by this method. Thus SIMPSON (1951) found the fecundity to be about 140 eggs per g. and estimated the total egg production in 1948 to be about $8 \times 10^{12}$ (SIMPSON, 1952), this being based on the assumption that the spawning in the Southern Bight accounts for about half the total plaice egg production in the North Sea. The recent work of BOHL (1954) indicates that this assumption may not be much wrong. From these figures the total weight of mature female plaice in that year was about

$$\frac{8 \times 10^{12}}{140} = 5{\cdot}7 \times 10^{10}\,\text{g}.$$

The European catch of plaice in 1948 was $8{\cdot}4 \times 10^{10}$ g., and from the sex composition and maturity data given by THURSBY-PELHAM (1939) it is probable that something between a quarter and half of this, by weight, consisted of mature females. Hence the ratio of catch to total population of mature females lies between the limits

$$\frac{2{\cdot}1 \times 10^{10}}{5{\cdot}7 \times 10^{10}} = 0{\cdot}37, \text{ and } \frac{4{\cdot}2 \times 10^{10}}{5{\cdot}7 \times 10^{10}} = 0{\cdot}74$$

This is not inconsistent with the pre-war value of $F$ of about 0·7 estimated from age composition data, remembering that the total fishing effort in 1948 may not have been quite as large as in the years immediately before the war, and that there is some indication that mature female plaice may be less liable to capture than mature males. With a comprehensive survey of egg production and contemporary sampling of the European plaice catch for sex ratio and maturity of females, it is reasonable to suppose that $F$ could be estimated to within limits narrower than those above.

There are, of course, certain difficulties with this method, although these are of a kind quite different from those encountered previously. They may include the identification of egg stages for the estimation of egg production, the estimation of fecundity and the distinction between mature and immature fish in catch samples. On the other hand, the estimate of

$F$ obtained in this way is entirely independent of natural mortality, it does not require indices of abundance (i. e., catch per unit effort) or catch sampling for either age or length distribution, and because it applies to a period of one year it is unaffected by fluctuations in year-class strength and fishing effort. It is important to note that if the commercial gear is differentially age-selective this method gives an estimate of $F$ which is an average of the values for the age-groups in question weighted by the relative catch (in weight) of each age-group; thus it lies *within* the range of the actual trend in $F$ (see section 5 (i)). Where egg surveys are practicable, estimating fishing mortality in this way at infrequent intervals, say every ten years or so, may provide a valuable independent check on the conventional catch sampling methods and perhaps deserves more attention than it has received hitherto.

### 6 (iii). Estimation of the area "swept" by the fishing gear.

The basis of this method, which was first used by Baranov (1918), is that since $F$ is a known function of the probability that a fish will be caught during a given period, it may be possible to estimate this directly by computing the area covered by the gear during a year. It may therefore be applicable to towed gears in which the area swept during a haul can be calculated from the dimensions of the gear and the distance towed, provided the whole of the fish population is within the range of the gear—both horizontally and vertically—while fishing is in progress. Suppose the area occupied by the fish population is $A$ and, in the first instance, that fish are distributed uniformly over it. Suppose also that each unit haul of the gear sweeps an area $a$ and catches the fraction $p$ of all fish lying in its path. If there are initially a total of $N_0$ fish, then after $n$ hauls have been made at random over the area the number of fish remaining, ignoring natural mortality, is

$$N_1 = N_0\left(1 - \frac{ap}{A}\right)^n$$

Put $\frac{an}{A} = k$; the number remaining is then

$$N_1 = N_0\left(1 - \frac{pk}{n}\right)^n \qquad (13)$$

Now if $n$ is very large, e. g., is the total number of hauls made during a year by the fleet, (13) becomes

$$N_1 \simeq N_0 e^{-pk}$$

Comparison with (18) of Appendix A shows that the quantity $pk$ is identical to the fishing mortality coefficient $F$, so that we have

$$F = \frac{pan}{A} \qquad (14)$$

This result remains valid when natural mortality is taken into account.

There are two main sources of error in estimating $F$ in this way. One is that neither fish nor fishing are ever uniformly distributed over the whole area, the tendency being for fishing to be most intense where fish themselves are most concentrated. Thus the majority of hauls will take a larger fraction of the total population than if fish and fishing were uniformly distributed, and $F$ will tend to be under-estimated by (14). This bias can be partially corrected if commercial statistics of catch and effort for sufficiently small sub-areas are available (e. g., statistical rectangles for demersal fish in the North Sea). The area swept per year in each sub-area could then be computed and $F$ estimated from the weighted sum of these swept areas, the weighting coefficient for each sub-area being the ratio of the density in it to the average density over all sub-areas.[1]) There remains, however, the difficulty that fish are unlikely to be uniformly distributed even within the smallest practicable sub-area and some may be on rough ground that is unfishable.

The other problem is that of estimating the value of $p$ in (14), i. e., the proportion of fish in the area swept in each haul that are caught by the gear. By assuming complete retention, i. e., by putting $p = 1$, Baranov obtained an estimate of $F$ of about 0·4 for North Sea plaice prior to the first world war. As far as can be judged from the limited effort statistics available for that period this figure is probably not far wrong, but as no allowance was made for the non-uniform distribution of fish and fishing it may be that this largely counteracted what would otherwise have been an over-estimate of $F$. The problem of estimating $p$ may be solved for some gears and species by developments in underwater photography, television, or other instruments of detection; in these circumstances and provided adequate commercial statistics of catch and effort are available, it should be possible to obtain a reasonably accurate estimate of $F$ in this way.

It is worth noting that in essence both this method and that of 6 (ii) involve estimation of the stock size by sample census. Of the two methods the latter, where applicable, has much in its favour because sampling of eggs is effected by research vessels—and only over a short period—so that control over the process is exercised, and also because the sampling efficiency of the plankton net is easier to study and usually higher than that of the fishing gear. However, it is not inconceivable that in, for example, purse-seine fisheries where the gear may take an entire shoal, giving virtually no chance of escape, echo-surveys to enumerate shoals may lead to successful use of the "swept-area" method.

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[1]) This procedure is exactly analogous to the computation of the effective overall fishing intensity $\tilde{f}$ (see Beverton and Parrish, No. 8).

## 7. Summary.

(i) This paper reviews the methods at present available for estimating mortality rates in exploited fish populations. Mortality estimation is an essential part of any study of fishery dynamics and is considered here because it makes the greatest demand on the sampling programme; indeed, it may often be the deciding factor in planning that programme.

(ii) Mortality rates are derived quantities that cannot be observed directly but have to be deduced from sample data with the help of theoretical population models. Reasons are given for representing mortality by instantaneous coefficients, and the relation of these to other measures of mortality are shown. Of particular importance is the fact that the instantaneous fishing mortality coefficient, $F$, is proportional to the fishing effort, provided the latter is computed in the appropriate way.

(iii) The estimation of mortality from age and length frequencies in catch samples is considered first. This information can be used only in the simple case when both $F$ and the instantaneous natural mortality coefficient, $M$, are constant, and gives an estimate of the total mortality coefficient $(F + M)$.

(iv) The separate estimation of $F$ and $M$ from catch samples requires the age structure to be expressed in terms of abundance indices (i. e., catch of each age-group per unit effort). It is also necessary that $F$ should have changed in a known way, either with time (as a result of known changes in fishing effort) or with age of fish (as a result of differential gear selectivity or fleet concentration). Attention is drawn to the importance of periods when $F$ is zero; either for part of the year, as in a seasonal fishery, or for several years, as happened in the North Sea during the war.

(v) The errors that may be introduced in mortality estimates if there are unsuspected trends in $F$ are illustrated by hypothetical examples. Most serious are trends in $F$ with age due to differential selectivity of the commercial fishing gear when the same gear is used for catch sampling and is thought to be non-selective. It is shown that in this case apparent age compositions may well be obtained that are indistinguishable in practice from ones produced by a constant $F$, but which if interpreted in this way can give entirely erroneous estimates.

(vi) Three other methods of estimating mortality rates are discussed briefly from the point of view of their use in detecting or avoiding bias that may be present in catch samples. These methods involve analysis of tagging experiments, computation of the ratio of catch to total population, or estimation of the area swept by the gear. The last two give an estimate of $F$ only, and this has to be subtracted from the estimate of $(F + M)$ by catch sampling to give $M$. Tagging experiments can, in theory, be used by themselves to estimate both $F$ and $M$, but the results are liable to bias from most of the factors influencing the catch sample methods and some additional ones peculiar to tagged fish. It is suggested that a useful technique may be to conduct tagging experiments simply to measure differential gear selectivity or fleet concentration, which is much easier than estimating $F$ or $M$ in absolute units; this information applied to catch sample data may enable a separation of $F$ and $M$ to be made that would not otherwise be possible.

(vii) Some of the methods described are illustrated by application to the stock of plaice in the North Sea, and it is shown that they give reasonably consistent results. For the period 1930—39, $F$ was about 0·7 and $M$ about 0·1.

(viii) It is emphasized that, in the first instance at least, as many as possible of the different methods of estimating mortality should be used and the results compared, because of many sources of bias that may be present in any one method. It is suggested that a research programme to estimate fishing and natural mortality rates can be based primarily on catch sampling, supplemented with standardized statistics of commercial fishing effort and, if possible, with comparative fishing and tagging experiments to investigate the sampling properties of the fleet and its gear. Egg surveys to estimate the true abundance of the population may provide, at intervals, a valuable independent check on the mortality estimates obtained by routine catch sampling.

# Appendices.

## Appendix A.

Let the total number of fish at the beginning of a year be $N_0$. With constant instantaneous fishing and natural mortality coefficients $F$ and $M$, the number present at any time $t$ during the year is

$$N_t = N_0 e^{-(F+M)t} \tag{15}$$

where $t$ is measured from the beginning of the year. The number remaining at the end of the year is therefore

$$N_1 = N_0 e^{-(F+M)} \tag{16}$$

Hence the *annual total mortality rate* and *expectation of death* is

$$\frac{N_0 - N_1}{N_0} = 1 - e^{-(F+M)}$$

and the *annual survival* rate is $e^{-(F+M)}$

The annual number caught is

$$Y_n = F\int_0^1 N_t\,dt = \frac{FN_0}{F+M}(1 - e^{-(F+M)}) \tag{17}$$

Hence the *annual expectation of capture* ($\equiv$ "rate of exploitation") is

$$\frac{Y_n}{N_0} = \frac{F}{F+M}(1 - e^{-(F+M)})$$

Similarly, the *annual expectation of natural death* is

$$\frac{M}{F+M}(1 - e^{-(F+M)})$$

The *annual fishing rate* has been defined as the fraction of the fish present at the beginning of a year that would be caught during the year if no other causes of death were operative. In this case, instead of (16) we have

$$N_1 = N_0 e^{-F} \tag{18}$$

so that the annual fishing rate is

$$\frac{N_0 - N_1}{N_0} = 1 - e^{-F}$$

Similarly, the *annual natural mortality rate* is $1 - e^{-M}$.

Instantaneous coefficients and expectations of death relating to specific causes can be simply added together to give the total value for all causes of death; this is not the case with the annual fishing and natural mortality rates.

## Appendix B.

Expressions for the mean age and length of fish in the catch above age $t'$ and corresponding length $l'$, can be derived by considering a year-class after it has entered this phase of the population. Its numbers at any age $t \geqslant t'$ are defined by (15), so that the number caught throughout the period from $t = t'$ to $t = \infty$ is

$$Y_n = F\int_{t'}^{\infty} N_t\,dt$$

The total age of all fish caught is

$$F\int_{t'}^{\infty} t\,N_t\,dt$$

Hence the mean age of fish in the total catch from the year-class between ages $t'$ and $\infty$ is

$$\bar{t} = \frac{F\int_{t'}^{\infty} t\,N_t\,dt}{F\int_{t'}^{\infty} N_t\,dt} \tag{19}$$

Substituting for $N_t$ from (15) and integrating, gives

$$\bar{t} = t' + \frac{1}{F+M}$$

For a population in a steady state this is also the average age of fish above age $t'$ in the annual catch.

An expression for the mean length of fish in the catch can be derived in a similar way. Thus, instead of (19) we have

$$\bar{l} = \frac{F\int_{t'}^{\infty} N_t\,l_t\,dt}{F\int_{t'}^{\infty} N_t\,dt}$$

Substituting for $l_t$ from the von Bertalanffy growth equation

$$l_t = L_\infty(1 - e^{-K(t-t_0)}) \tag{20}$$

and for $N_t$ from (15) and integrating gives

$$\bar{l} = L_\infty\left(1 - \frac{F+M}{F+M+K}e^{-K(t'-t_0)}\right) \tag{21}$$

However, from (20) the length of fish at age $t'$ is

$$l' = L_\infty(1 - e^{-K(t'-t_0)})$$

from which

$$e^{-K(t'-t_0)} = \frac{L_\infty - l'}{L_\infty}$$

Substituting in (21) and rearranging gives

$$F + M = \frac{K(L - \bar{l})}{\bar{l} - l'}$$

## Appendix C.

For a population defined by (15), the mean number present during the first year is

$$\bar{N}_1 = \frac{\int_0^1 N_t dt}{\int_0^1 dt}$$

Since the denominator is unity we have

$$\bar{N}_1 = \frac{N_0}{F + M}(1 - e^{-(F+M)}) \qquad (22)$$

At the end of the first year the survivors will number

$$N_1 = N_0 e^{-(F+M)}$$

Their annual mean abundance during the following year is, similarly,

$$\bar{N}_2 = \frac{N_0 e^{-(F+M)}}{F + M}(1 - e^{-(F+M)}) \qquad (23)$$

Hence

$$\log_e\left(\frac{\bar{N}_1}{\bar{N}_2}\right) = (F + M)$$

so that provided $F$ and $M$ are constant through both years the annual mean abundances give a true estimate of the total mortality coefficient $(F + M)$.

## Appendix D.

Suppose a year-class enters age-group $v$ at the beginning of year $x$, when its numbers are ${}_vN_x$. Its mean abundance during year $x$, when the fishing intensity is $\tilde{f}_x$ is given from (22) by the expression

$${}_v\bar{N}_x = \frac{{}_vN_x}{c\tilde{f}_x + M}\left(1 - e^{-(c\tilde{f}_x + M)}\right) \qquad (24)$$

Similarly, its mean abundance in the following year $x + 1$, when the fishing intensity is $\tilde{f}_{x+1}$, from (23), is

$${}_{v+1}\bar{N}_{x+1} = \frac{{}_vN_x\ e^{-(c\tilde{f}_x + M)}}{c\tilde{f}_{x+1} + M}\left(1 - e^{-(c\tilde{f}_{x+1} + M)}\right) \qquad (25)$$

Dividing (24) by (25) and taking natural logarithms gives

$$\log_e\left(\frac{{}_v\bar{N}_x}{{}_{v+1}\bar{N}_{x+1}}\right) + \log_e\left\{\frac{(c\tilde{f}_x + M)(1 - e^{-(c\tilde{f}_{x+1} + M)})}{(c\tilde{f}_{x+1} + M)(1 - e^{-(c\tilde{f}_x + M)})}\right\} = c\tilde{f}_x + M \qquad (26)$$

The same equation is obtained if the catch per unit effort of each age-group is used as an index of its true abundance, provided both are sampled with equal efficiency.

The second logarithmic term of the left hand side is the term $Q_{(10)}$ of (10), referred to in section 4 (ii). Solutions for $c$ and $M$ are obtained by successive approximation. Thus if the term $Q_{(10)}$ is ignored we have

$$\log_e\left(\frac{{}_v\bar{N}_x}{{}_{v+1}\bar{N}_{x+1}}\right) \simeq c\tilde{f}_x + M$$

and plotting the log ratio of abundance in pairs of years against the fishing intensity in the first year of each pair, $\tilde{f}_x$, gives first estimates of $c$ (slope) and $M$ (intercept). These are then used to compute approximate values of $Q_{(10)}$ for each pair of years, which can then be added to the corresponding log-abundance ratios and the whole of the left hand side of (26) replotted against $\tilde{f}_x$. This gives more exact estimates of $c$ and $M$, the process being repeated until there is no appreciable difference in successive estimates of these parameters. Examples of the application of this method are given by Beverton and Holt (in press).

Additional terms for (11) and (12), in which $F$ varies with age as a result of differential gear selectivity, can be deduced and used in an exactly similar way. For (11) the correction term is

$$Q_{(11)} = \log_e\left\{\frac{(y_{v+r} \cdot F_v + M)\{1 - exp(-y_{v+r+1} \cdot F_v - M)\}}{(y_{v+r+1} \cdot F_v + M)\{1 - exp(-y_{v+r} \cdot F_v - M)\}}\right\}$$

and for (12) it is

$$Q_{(12)} = \log_e\left\{\frac{(z_{v+r} \cdot {}_AF_v + M)\{1 - exp(-z_{v+r+1} \cdot {}_AF_v - M)\}}{(z_{v+r+1} \cdot {}_AF_v + M)\{1 - exp(-z_{v+r} \cdot {}_AF_v - M)\}}\right\}$$

## Appendix E.

Consider a year-class entering age-group $v$ and numbering $N_v$ fish, that is then fished by a differentially selective gear. If the fishing mortality coefficient while in age-group $v$ is $F_v$, then the catch in numbers of the year-class while in that age-group is given from (17) as

$${}_vY_n = \frac{F_v \cdot N_v}{F_v + M}(1 - e^{-(F_v + M)})$$

and that from the same year-class when in any subsequent age-group $v + r$ is

$$_{v+r}Y_n = \left(\frac{F_{v+r}\,N_v}{F_{v+r}+M}\right)\left\{1-exp\,(-F_v-M)\right\}\times$$

$$\times\ exp\left\{-\sum_{p=v}^{v+r-1}(F_p+M)\right\} \qquad (27)$$

The true annual mean abundance of the year-class when in age-group $v+r$ is

$$\bar{N}_{v+r} = \frac{_{v+r}Y_n}{F_{v+r}} \qquad (28)$$

a proportional index of which would be obtained from the catch per unit effort of a non-selective gear.

If, however, the catch per unit effort of the differentially selective gear is used to estimate abundance, but the gear is thought to be non-selective, the catch of each age-group will be divided by the same unit of effort whereas, in fact, an adjusted effort should have been used according to the change in $F$ with age (see (28)). In this case the age composition of the catch is not the same as that of the population. In Fig. 2 the population age compositions (●) have been calculated from (28) and those of the catch (○) from (27).

**Appendix F.**

Suppose that $N_0$ tagged fish are liberated in a batch, and that the subsequent decrease in their numbers can be represented by a fishing mortality coefficient $F$ and an "other-loss" coefficient $X$, both being constant. The number recaptured in a period of duration $\tau$ after liberation is given from (17) as

$$n_1 = \frac{FN_0}{F+X}(1-e^{-(F+x)\tau}) \qquad (29)$$

while the log ratio of $n_1$ to the number recaptured in the next period of similar duration, $n_2$, is

$$\log_e\frac{n_1}{n_2} = (F+X)\,\tau \qquad (30)$$

(see (22), (23) and (28)). Substituting for $(F+X)$ from (30) in (29) gives

$$F = \frac{\frac{n_1}{\tau}\log_e\frac{n_1}{n_2}}{N_0\left(1-\frac{n_2}{n_1}\right)} \qquad (31)$$

The estimation of fishing mortality from tagging data by this or similar methods has been discussed by Ricker (1948), Beverton and Holt (in press) and Jones (Contribution No. 4).

**Addendum.**

Since this paper went to press, T. M. Widrig has published an estimation of the fishing and natural mortality rates in the California sardine, using methods which are basically the same as those outlined in section 4 (ii) with fishing effort varying from year to year. The details of application, however, are dealt with more fully than has been possible here, and some further practical problems arising in estimating mortalities in migratory populations are discussed. The publication in question is, T. M. Widrig: "Method of estimating fish populations, with application to Pacific sardine". U. S. Fish and Wildlife Service, Fish. Bull., 94, 1954.

## 10.

# A Comparison of Brood-Strength Fluctuations in the Immature and Mature Parts of the Arcto-Norwegian Cod Population.

*By* GUNNAR SÆTERSDAL

THE fluctuation in the Arcto-Norwegian stock of cod has been the subject of intensive investigations (SUND, ROLLEFSEN and others). These investigations have been based mainly on observations of the mature part of the stock: the skrei. It is, however, of considerable interest to extend such investigations to younger age-groups.

Besides the Lofoten fishery we have another Norwegian seasonal cod fishery: the spring cod fishery in Finnmarken during the months April to June. By an analysis of length measurements from a series of years SUND has shown that this fishery is based on the immature part of the Arcto-Norwegian cod population.

That the skrei and the spring cod belong to the same population can also be shown by comparing the yield per effort curves of the two fisheries. Figure 1 shows that there is a difference of 3 to 4 years in the fluctuations of the two curves. This is in accordance with the difference in average age of the spring cod and the skrei.

The age distribution of samples of cod from the spring cod fishery is influenced by a number of factors, the most important of which are probably the following:—

1) The selection when sampling the catches.
2) The selection by the gear used.
3) The rate of mortality and maturity in the spring cod population.
4) The recruitment of the various year-classes to the shoals of spring cod migrating to the Finnmarken area.

The selection by sampling can be excluded by sampling total catches when this is possible.

The dominating gear in the spring cod fishery is the long-line. The selective effect of this gear is probably one of size only. Figure 2 shows typical length

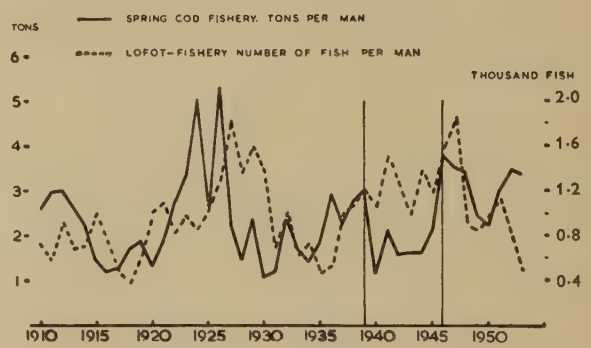


Figure 1. The yield of the spring cod fishery in tons per man and the Lofoten fishery in number of fish per man.

distribution curves of catches taken by trawl and by long-lines at the Finnmarken banks in May 1953. Probably neither of these represent the true length distribution of the population, but we may assume that the trawl catch gives us by far the best idea of it. For the purpose of determining the brood-strength variations it is, however, not necessary to know the true size or age distribution of the population. If the selective effects of the different gears are always the same, it is sufficient to compare catches from the same gear. The selectivity of the long-lines in respect of fish size is probably constant. But if the size/age relationship in the population changes, the selectivity of the long-lines with respect to age will also change. Such changes can, however, be detected by means of growth studies.

Changes in the mortality and age at first maturity may undoubtedly lead to significant changes in the age distribution. Nothing is known of the mortality rate at present, but the age at first maturity can be determined at Lofoten.

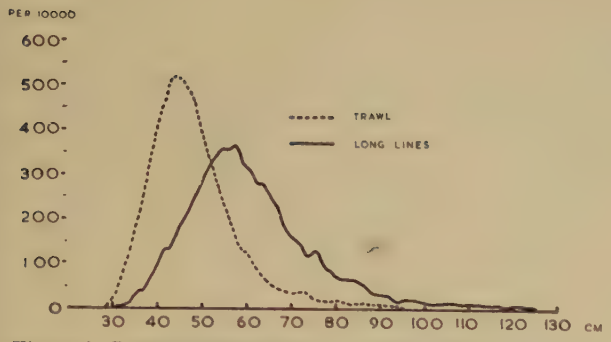


Figure 2. Length distributions of catches from trawl and from long-lines. Finnmarken, May 1953.

Regarding point 4 it must be presupposed that the recruitment to the spring cod population occurs according to a definite law as a fairly constant percentage of each age-group of the total cod population, and consequently is proportional to the strength of the various year-classes.

Several other factors may influence the age distribution. For instance, there seems to be a selection with depth as catches from shallower waters usually contain a higher proportion of younger fish than those from deeper waters. This especially concerns three- and four-year-old fish, and these age-groups have been omitted in the following calculations.

It must also be mentioned that in the spring cod catches there is always some intermingling of skrei returning from the spawning migration. These mature fish can, however, be removed from the material if the state of the gonads is observed.

This reasoning leads to the conception of an average "normal" age distribution of the spring cod, influenced mainly by changes in the rate of mortality and maturity. By comparing each year's age distribution with the average distribution for a series of years it is possible to get an estimate of the strength of each year-class in relation to the adjacent ones, that is, an estimate of the fluctuations above and below the average strength of the year-classes in these years. A change in this average cannot be observed unless the relative strength of the year-classes can be related to the yield and the fishing intensity in the corresponding years.

The yield of the spring cod fishery is known. The fishing intensity is a variable that is dependent upon the number of fishermen engaged in the fishery, the gears and methods used, the weather conditions, and probably several other less important factors, the influence of which we have no means of evaluating. The influence of the weather conditions has been omitted in this preliminary investigation. The gears and methods can be considered as being constant in the relevant period. However, in the latest years the trawl has been introduced as a new gear in this fishery, and its increasing use may complicate future calculations. In the following calculation the number of fishermen has been used as a measure of the fishing intensity; and accordingly, the yield per fisherman as a measure of the abundance.

The period of age observations covers the years 1934 to 1939 and comprises a total of 2361 observations. Table 1 shows the yield in kilos per fisherman of each year-class in the interval 5 to 10 years and the average yield of each age-group in the years 1934 to 1939. Table 1 also shows the total yield of each year-class as a percentage of the sum of the average yield in the corresponding age-groups. Rollefsen has for a series of years used a similar method in evaluating the brood-strength fluctuations in the skrei population at Lofoten. For comparison his data are listed in the table. The two sets of data cover the same year-classes, but the calculations are not based on corresponding averages and are, therefore, not directly comparable. A more independent expression of the fluctuations of the year-classes can be formed by calculating the quotients between each year-class and the preceding one. These quotients (listed in Table 1) show that the year-classes 1929 to 1932 fluctuate in almost exactly the same way in the two sets of data.

*Such close agreement is a strong indication that our observations of the fluctuations in the strength of the year-classes 1929 to 1932 are reliable both in the Lofoten and in the Finnmarken material.* That the strength of these year-classes, when related to the respective averages used, are not the same, can be explained by the fact that the averages, as has been mentioned before, do not correspond. In the Lofoten material each of the year-classes has been observed during six years, while in the Finnmarken material the observation period varied from one to six years.

In order to facilitate the comparison, one of the "reliable" year-classes in the period 1929—1932 can be used as a common standard. In Table 1 the strength of the 1930 year-class in the Finnmarken data has been made equal to the Lofoten observation and the rest of the Finnmarken data recalculated in accordance with this. The results are illustrated in Figure 3. The year-classes 1929 to 1932 agree closely, while as a whole the "Finnmarken year-classes" 1924 to 1928 are smaller and those from 1933 and 1934 larger than the "Lofoten ones". The lack of agreement is in itself not unexpected, because the number of Finnmarken observations of these year-classes are small. The tendency of the disagreement is more difficult to explain. The relative underrating of the earliest year-classes in Finmarken may be caused by a change in the age at first maturity. According to Rollefsen the average age at first maturity of the Lofoten skrei increased about $^1/_2$ to $^3/_4$ year in the years 1938 to 1940. The overrating of the latest year-classes may actually be a sort of underrating of the same year-classes in Lofoten caused by an increased mortality in the stock of spring cod, possibly as a result of the heavy increase in the trawl fishery in these years.

There is also some information on line-caught cod from the Spitsbergen banks: a total of 3915 observations covering the years 1937 to 1939. This material has

**Table 1.**

**Spring Cod Fishery. Yield in Kilos per Fisherman of each Year-class at the available Ages in the Interval 5—10 Years, and the total Yield as per cent. of the Average in the Years 1934—1939 compared with Observations from Lofoten (ROLLEFSEN) and Spitsbergen.**

| | Finnmarken. Yield in kilos per fishermen. | | | | | | Finnmarken 5—10 years | | Lofoten 8—13 years | | Finm. recalc. | Spitsbergen 4—11 years | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year-class/Age | 5 | 6 | 7 | 8 | 9 | 10 | % of average | Quot. $\frac{1925}{1924}$ etc. | % of average | Quot. | 1930 equal | % of average | 1930 equal |
| 1924 ..... | .. | .. | .. | .. | .. | 8 | 16 | | 34 | | 18 | .. | .. |
| 1925 ..... | .. | .. | .. | .. | 39 | 44 | 37 | 2·32 | 40 | 1·18 | 41 | .. | .. |
| 1926 ..... | .. | .. | .. | 187 | 63 | 32 | 45 | 1·22 | 80 | 2·00 | 50 | .. | .. |
| 1927 ..... | .. | .. | 233 | 165 | 80 | 43 | 41 | 0·91 | 100 | 1·25 | 46 | 28 | 35 |
| 1928 ..... | .. | 428 | 342 | 509 | 173 | 71 | 81 | 1·98 | 116 | 1·16 | 90 | 81 | 101 |
| 1929 ..... | 373 | 488 | 1,177 | 471 | 313 | 105 | 133 | 1·64 | 150 | 1·29 | 149 | 129 | 161 |
| 1930 ..... | 495 | 1,001 | 909 | 754 | 346 | .. | 162 | **1·22** | 181 | **1·21** | 181 | 145 | 181 |
| 1931 ..... | 64 | 374 | 664 | 322 | .. | .. | 72 | **0·44** | 78 | **0·48** | 80 | 58 | 72 |
| 1932 ..... | 128 | 360 | 579 | .. | .. | .. | 67 | **0·93** | 74 | **0·95** | 75 | 98 | 122 |
| 1933 ..... | 417 | 1,029 | .. | .. | .. | .. | 155 | 2·31 | 120 | 1·62 | 173 | 90 | 112 |
| 1934 ..... | 466 | .. | .. | .. | .. | .. | 144 | 0·93 | 113 | 0·94 | 161 | 120 | 150 |
| Average ..... | 324 | 613 | 651 | 401 | 169 | 51 | | | | | | | |

been treated in the same way as that from Finnmarken, but as the fishing intensity in this area was unknown, no measure of abundance has been used when calculating the strength of the year-classes. Table 1 shows the strengths of the year-classes as percentages of the average for 1937 to 1939 and, for comparison with the Lofoten material, recalculated with the 1930 year-class equal to the Lofoten 1930 year-class. The result is illustrated in Figure 3. In the case of the year-classes 1928 to 1931 there is seen to be a fair agreement with the calculations for Lofoten and Finnmarken.

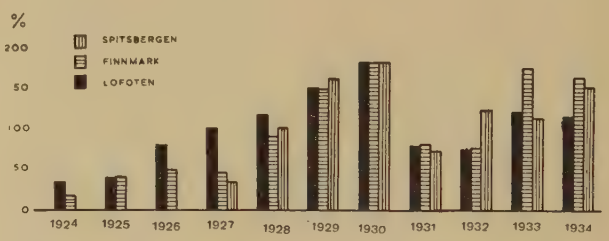


Figure 3. Relative strength of the year-classes 1924 to 1934 as observed in Lofoten 1932—1947, in Finnmarken 1934—1939 and at Spitsbergen 1937—1939, cf. Table 1.

## 11.

# Problems of Sampling a Puget Sound Population of English Sole, *Parophrys vetulus*[1]).

*By* Richard Van Cleve *and* Alonzo T. Pruter

Since the development by Baranov (1918) of a mathematical theory of the reactions of a fish population to a fishery and its application by Thompson and Bell (1934) to the halibut fishery, a number of attempts have been made to develop a more precise mathematical formulation and to apply the theory to other fisheries. These attempts have met varying degrees of success. In general because of the exploratory nature of most fisheries research it has not produced a sufficiently complete and consistent body of data for use in refined mathematical relationships. Inaccuracies arise from a lack of adequate measures of most, if not all, of the parameters on which the population equations are based, but in spite of all such errors results have been encouraging (Beverton, 1953; Schaefer, 1954).

To simplify the mathematical concepts and equations, all treatments of the problem have followed methods developed for controlled experiments describing variations in yield that would occur with changes in only one of the parameters of interest, such as fishing intensity, natural mortality, or age at recruitment, while the other parameters affecting yield or population size are held constant. Interaction between the competing rates has been mentioned but lack of data has prevented elucidation except on a purely hypothetical basis. In all cases both recruitment and growth have been treated as constant rates unaffected by changes in population size. The resultant curves that have been developed to describe the "equilibrium yield" (Beverton, 1953, and others) under different conditions for different species have therefore been unrealistic and in fact completely uninterpretable in terms of what would actually occur under natural conditions. The closest approach to reproducing these conditions was made by Thompson and Bell (1934) with their simple arithmetic treatment of individual year-classes.

Lack of realism stems first from the difficulty of developing mathematical hypotheses that can be solved without oversimplification of basic concepts as noted above. Data are usually available which permit assignment of values to annual amounts of fishing effort and total catch. In addition total catch and hence total effort, are the variables most accessible to artificial modification. Detection of changes in growth-rate or natural mortality would involve extensive studies of any species and suitable data are not available except to those able or willing to execute such investigations. However, the great differences in growth of plaice on the Dogger Bank as compared with those living under more crowded conditions on the Flemish coast (Hickling, 1937) indicate that changes in growth rate may be one of the major variables determining changes in productivity of a stock. Recent observations on the Pacific halibut have indicated an increase of almost 100 % in weight of mature females of comparable ages since the first observations were made in area 3 in 1926 (International Pacific Halibut Commission Report No. 21, 1954). This growth increase did not occur instantaneously as the stocks in that area were reduced, but required some 17 years to develop after the time that the abundance had begun to increase from the low population level of 1930. Assumption of constant recruitment for the purposes of mathematical treatment is also untenable in the light of available information but no fishery seems to be well enough documented to indicate how recruitment will

1) Acknowledgements. The work summarized briefly below comprises a joint project of the University of Washington School of Fisheries and the Washington State Department of Fisheries. Many people are participating in the field work and reports by all principal participants covering the phases of their interest will be published as the analysis of data progresses. The work of the University of Washington has been partially supported by funds allocated to this project under State Initiative 171.

vary with changes in population size. Major changes are also inevitable in natural mortality rates as population sizes are reduced or increased and must inevitably be measured to ascertain the true potentialities of our fish populations.

The second way in which current theoretical treatments of fish population dynamics depart from reality is in considering productivity in terms of "equilibrium catch" or yield. While this is probably necessary to permit simplification of mathematical treatment it must be recognized that equilibrium is seldom attained in any fishery for a sufficient period to establish the size of the equilibrium yield at any level of fishing. As an example, the delayed reaction of both recruitment (Thompson, 1950) and growth in the halibut may be greater than in other species where maturity is reached at an earlier age but it must be present in varying degrees in all fisheries. Use of the available data on yield and average catch per unit of effort without evaluation of the other changes that are related to them can thus lead to results that may be quite misleading. For example Schaefer (1954) calculated the maximum stabilized yield of the area 2 halibut fishery as 28·2 million pounds at an average abundance of 78 pounds per skate, although this fishery has for several years past exceeded both this yield and abundance. Other considerations involving distribution of the Pacific halibut fishery and the progressive shortening of the fishing season since 1930 indicate that the true figures are probably higher than Schaefer's estimates. The dangers of misinterpretation of results obtained by using so-called "equilibrium yield" curves to describe the manner in which a fish population will react to a fishery must be recognized.

The need for observations planned and collected specifically to fit into the conditions required for population investigations has long been felt and a search for a suitable fish population in Puget Sound has been in progress for some years. The discovery of what appears to be an isolated population of limited extent of *Parophrys vetulus*, the so-called "English sole", in the passages and bays to the eastward of Whidbey Island (Figure 1), which supports a trawl fishery small enough to be easily observed has led to the development of the present programme. The authors plan to observe this fishery to discover how recruitment, growth, natural mortality, fishing mortality, and other variables are related to yield and to the accumulated population. The relation of the *Parophrys vetulus* stock to other species in the area may shed much light on similar situations in which one or two species are exploited heavily with only casual interest in other fish.

Before the more detailed development of estimates of population parameters which will appear in later publications it is of interest to consider the adequacy of our present system of sampling as well as various problems that have arisen while devising methods of obtaining data that will permit evaluation of the sources of error.

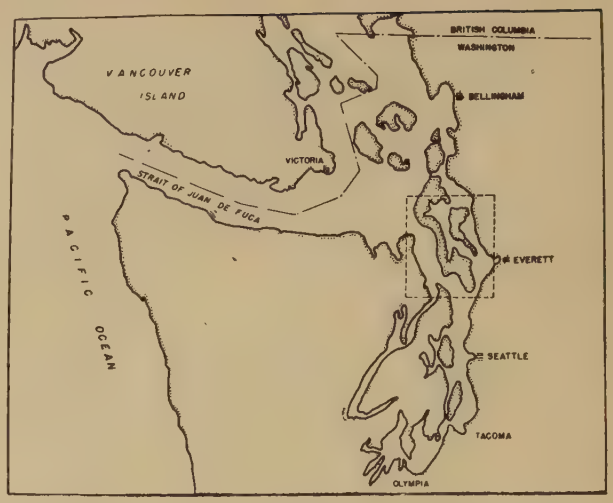


Figure 1. Location of study area in Puget Sound, Washington.

## The Fishery.

Forty-seven species of fish have been recorded by the University of Washington's research vessel, M. V. "Oncorhynchus", in Penn Cove, Saratoga Passage and Holmes Harbor in 1952—53 (Table 1). All of these species are caught by commercial trawlers but only eight are landed in quantity for human consumption. However, large numbers of hake, pollack, skates, and dogfish are sold to reduction plants. The remaining 35 species are either uncommon, relatively unavailable to trawls, or are too small to be caught in quantity with the mesh size used by the commercial boats. Therefore a true picture of the species composition cannot be obtained from an examination of the commercial catches but instead requires sampling with nets of various mesh sizes such as those used by the M. V. "Oncorhynchus".[1])

The species in greatest abundance and demand is *Parophrys vetulus* which is found throughout most of the area in 5 to 110 fathoms, the depth varying both as to time and location. The presence of several desirable species in considerable numbers, the proximity of local markets, and the advantage of fishing in sheltered waters results in a rather intense winter trawl fishery by boats landing their fares in Seattle, Everett, and Bellingham (Figure 1). Vessels engaged in the fishery are of the ocean-going type, ranging in

[1]) The smallest mesh used in our nets is still large enough to permit the escape of small fish such as most *Aulorhynchus* and all *Sygnathus* which occur in great numbers in Puget Sound. Moreover, trawls do not adequately sample most pelagic species. It is hoped that funds will be found to develop methods for sampling these other species. Until they are sampled quantitatively and their relationship to the whole population complex determined, this gap will remain in our population picture. Filling this gap may be impractical, however, unless a fishery is built up to sample the pelagic species.

**Table 1. Species of Fish caught in Penn Cove, Saratoga Passage, and Holmes Harbor by the M. V. "Oncorhynchus" in 1952—53.** Important Food Fish denoted by Asterisk.

Pleuronectidae
**Parophrys vetulus* (English sole)
**Platichthys stellatus* (starry flounder)
**Lepidopsetta bilineata* (rock sole)
**Psettichthys melanostictus* (sand sole)
*Hippoglossoides elassodon* (flat-head sole)
*Lyopsetta exiles* (slender sole)
*Microstomus pacificus* (Dover sole)
*Eopsetta jordani* (petrale sole)
*Glyptocephalus zachirus* (rex sole)
*Pleuronichthys coenosus* (C-O sole)
*Atheresthes stomias* (turbot)
*Isopsetta isolepis* (Bellingham sole)

Bothidae
*Citharichthys sordidus* (mottled sand-dab)
*Citharichthys stigmaeus* (speckled sand-dab)

Scorpaenidae
**Sebastodes caurinus* (red rockfish)

Gadidae
**Gadus macrocephalus* (true cod)
*Merluccius productus* (hake)
*Theragra chalcogramma* (pollack)
*Microgadus proximus* (tomcod)

Embiotocidae
**Taeniotoca lateralis* (blue sea-perch)
*Damalichthys vacca* (dusky sea-perch)
*Cymatogaster aggregatus* (yellow shiner)

Hexagramidae
**Ophiodon elongatus* (ling cod)
*Hexagrammos stelleri* (white-spotted greenling)
*Zaniolepis latipinnis* (long-spined greenling)

Anoplopomidae
*Anoplopoma fimbria* (sablefish)

Agonidae
*Xenopyxis latifrons* (black-tipped sea-poacher)
*Agonus acipenserinus* (sturgeon-like sea-poacher)
*Odontopyxis trispinosus* (pigmy sea-poacher)

Cottidae
*Leptocottus armatus* (cabezon)
*Chitonotus pugetensis* (rough-backed sculpin)
*Dasycottus setiger* (spiny-headed sculpin)
*Radulinus asprellus* (darter sculpin)

Batrachoididae
*Porichthys notatus* (midshipman)

Zoarcidae
*Lycodopsis pacificus* (black-bellied eel-pout)

Aulorhynchidae
*Aulorhynchus flavidus* (tube-snout)

Clupeidae
*Alosa sapidissima* (shad)
*Clupea pallasii* (herring)
*Engraulis mordax* (anchovy)

Osmeridae
*Hypomesus pretiosus* (silver smelt)
*Thaleichthys pacificus* (eulachon)
*Spirinchus dilatus* (long-finned smelt)

Chimaeridae
*Hydrolagus colliei* (rat-fish)

Rajidae
*Raja rhina* (long-nosed skate)
*Raja binoculata* (big skate)

Scylliorhinidae
*Apristurus brunneus* (brown shark)

Squalidae
*Squalus acanthias* (dog-fish)

length from 50 to 85 feet and from 20 to 60 net tons capacity. Three men, including the captain, comprise the average crew. The trawl is set off the vessel's stern and brought aboard over the starboard side. The average net is about 350 meshes in circumference and the legal minimum mesh size is $4^1/_2$ inches (stretched measurement, opening between knots). However, some boats use nets as small as 275 and as large as 400 meshes in circumference and the mesh size varies from $4^1/_2$ to $5^1/_2$ inches. The effect of these variations in the trawls on the size of *Parophrys vetulus* caught is being studied by comparing length samples of the catches, with those taken in the markets, and with samples on the M. V. "Oncorhynchus". The samples of the catches are taken aboard the vessels before selection is exercised by the fishermen.

Reefs, logs, snags, and legal closures render a considerable portion of the region inaccessible to trawling, and the percentage of the trawlable bottom varies considerably in the different areas. For example, about 67 % of Holmes Harbor, 87 % of Penn Cove, 22 % of Saratoga Passage, and 68 % of Port Gardner can be fished (Figure 2). *Parophrys vetulus* and other species undoubtedly inhabit a considerably portion of the inaccessible areas. Their movements into and out of the accessible trawling grounds may be an important cause of some of the observed variations within the fishery.

To obtain accurate catch and tag recovery data the trawling grounds have been subdivided into numbered areas (Figure 2) and the captains have been requested to record the area, depth, and nature of their catches on special statistical forms supplied to them (Pruter and van Cleve, 1954). Besides providing for estimates of the pounds of individuals species of fish caught in each haul, the catch forms were designed so that the tag number of each tagged fish caught could be readily entered under the appropriate haul number. The

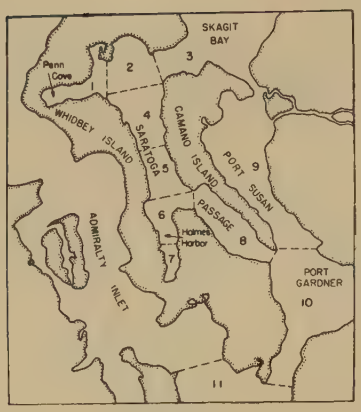


Figure 2. Detailed map of study area showing numbered catch areas.

catch records and information on tag recoveries have been supplied by the fishing boats without reward and their cooperation is largely responsible for the success of the programme. These forms provided a detailed record of 79 % of the total *Parophrys vetulus* taken in the study areas during the past season.

Penn Cove, Saratoga Passage, and Port Gardner have long been among the major Puget Sound trawling grounds. Over a number of years seasonal regulations have assumed a complex pattern. Trawling in Penn Cove and the upper half of Saratoga Passage (areas 1—5) has been restricted to a season which in 1953—54 extended from 15. September through 15. February. Trawling is permitted in the lower half of Saratoga Passage (area 8), Port Gardner (area 10) and Port Susan (area 9) at all times of the year except from 16. February to 14. April. Holmes Harbor (areas 6 and 7) was closed to trawling from 1937 through 1952. A six-week season was permitted in 1953 which extended from 1. January through 13. February, and a fishery was again allowed in Holmes Harbor in 1954, with a minor adjustment which extended the closing date to 15. February.

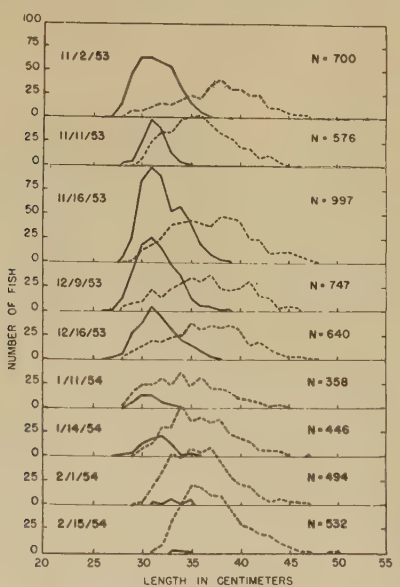


Figure 3. Length-frequencies of male and female *Parophys vetulus* obtained from market samples.

The complexity of the seasons has not been reflected in the activity of the fishing fleet since a large number of the vessels convert to other fisheries such as halibut and salmon, during the spring and summer months, and the remainder participate in the ocean trawl fishery at that time. The result is that the fishery in areas 1—10 is almost entirely restricted to the late autumn and winter months.

Sixteen vessels fished in areas 1—10 between 15. September 1953 and 15. February 1954 and landed about 600,000 pounds of fish, 445,000 pounds of which were *Parophrys vetulus*. An additional 600,000 to 1,000,000 pounds of scrap fish were sold to reduction plants. Total landings of all fish will be considered in assessing the productivity of the area but present studies are concentrated on the one species for which detailed records are available.

**Market samples.**

The fishermen normally discard all of the smaller *Parophrys vetulus*, keeping only those of legal size ($\geqslant$ 292 mm. in total length) but the degree of selection exercised by the fishermen varies with both the relative abundance and the demand for the fish. During periods of scarcity or high price, care is taken by the fishermen to keep all fish caught which are of legal size. When fish are abundant the fishermen sort their catches rapidly and tend to discard fish considerably above the legal minimum size. Since the male *Parophrys vetulus* are considerably smaller than the females, such varying selection by the fishermen causes changes in the sex ratio in the landings.

Unusually moderate winds during January and February of 1954 permitted trawlers to fish the ocean banks more intensively than normal at that time of the year. The consequent influx of the more desirable ocean-caught fish on the markets depressed the demand for Puget Sound fish, and the buyers progressively raised the minimum size limit on Puget Sound *Parophrys vetulus* after 11. January. The above is best shown by length frequencies of males and females caught in areas 1—10 and landed between 2. November 1953 and 15. February 1954 obtained from market samples (Figure 3). As may be seen from the figure, the sizes and sex ratios were fairly constant until 11. January. From that time on, however, the length of both males and females increased progressively with a marked change in the relative numbers of males which made up 40·6 % of the 16. December sample but only 1·5 % of the 15. February sample.

Significant changes of this type occur irregularly in many Pacific coast fisheries. Such changes can have a profound effect on the average size of fish landed and consequently on the calculated catch per unit of

fishing effort. Although such changes are economic rather than biological in origin they are just as real as biological changes and must not be confused with changes in population parameters.

The progressive increase in the minimum size limit of *Parophrys vetulus* accepted by the dealers during this season has made it necessary to adjust the catches of individual hauls as recorded to make them comparable with earlier catches, because as the size limit rose greater numbers of *Parophrys vetulus* had to be caught in order to obtain as many marketable fish as during previous periods. While smaller fish were discarded we have reason to believe most of them did not survive and they should be considered as part of the catch. The amounts by which the catches were corrected during the latter part of the season varied between 8 and 35 %. Sampling can be gauged to provide a sufficient amount of data to give statistically uniform results at any time. However, statistical techniques would not normally take into consideration the above changes and they would probably be overlooked in routine market sampling or in an analysis of catch per unit of effort.

**Selectivity of gear.**

The selective action of trawls is well known for some species but the adjustment of data to overcome this handicap has not been handled uniformly, and in some cases has not been handled well. Trawls that are designed to capture only the legal or marketable sizes of a particular species can give no idea of the nature of the age or size distribution of fish too small to be completely sampled. An adjustment is not valid which assumes that the probability of capture of fish below the size of complete availability is expressed by the ratios of distributions that have no relationship to the relative abundance of those sizes in the population. Unless the true population curve can be established at sizes below that of complete availability it seems best to confine attention for the present to sizes and ages above the critical point.

The difference in size of the two sexes of *Parophrys vetulus* poses a problem that is illustrated by the growth curves of males and females shown in Figure 4. These curves are composed of the combined distributions obtained from comparable catches made with trawls equipped with cod-ends of $1^1/_2$, $3^1/_2$, and $4^1/_2$ inch mesh. The minimum size limit of 292 mm. permits the landing of all females six years and older. However in our March 1954 samples it excluded some males as old as 14 years. Whether or not this will force us to consider only the females in our population studies can only be determined after further study of the effect of this selection on the relative mortality rates of the two sexes. The landings can be separated as to sex if sufficient labor can be assigned to market observations but this will be of little use without a thorough biological study of the stocks remaining on the grounds.

An important effect of net selection was seen in the

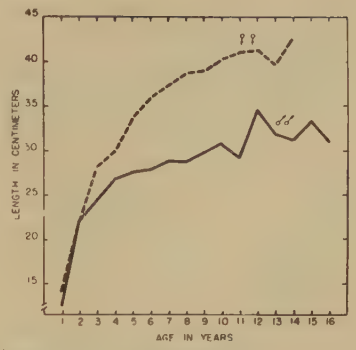


Figure 4. Age/length relationship of male and female *Parophrys vetulus*.

shapes of growth curves obtained from comparable hauls made with the three different mesh-sized cod-ends in the same area. An effect of the smaller meshes that is not often recognized is that they permit the escape of larger fish (Jurkovich, 1954). This probably results from the slower speed of dragging due to the greater resistance of the net and perhaps also to the more rapid clogging of the finer net with fish or debris thus decreasing the entering current speeds at the trawl mouth, allowing the larger, more rapidly swimming fish to escape. The resulting length distributions taken from each mesh size therefore yield different growth curves. The $4^1/_2$ inch mesh net, by permitting the escape of the smaller sizes of the younger ages, flattens the curve significantly especially for the males. Other differences are seen in the relative scarcity of larger fish in the $1^1/_2$ inch mesh hauls as well as in the absence of the first-year-fish and scarcity of two-year-olds in catches taken with the $3^1/_2$ and $4^1/_2$ inch meshes. Because of these differences in selectivity, samples from a single mesh size could hardly give an accurate measure of the growth rate. An attempt to obtain accurate growth data has been made by combining samples from different mesh sizes and weighting each sample to represent a standard area trawled.

The difference in growth rate between males and females and the resultant differences in net selection make it impossible to draw conclusions as to relative numbers in the different age-groups except from samples obtained with a variety of mesh sizes. Age frequencies of females in such samples obtained in March 1954 soon after the close of the fishing season show a regular decline after age six, indicating little variation in the strength of age-groups of females. A straight line fitting the logarithms of the age frequencies gives a survival rate of 47 %. The males on the contrary show wide variations in the strength of year-classes from age 7 to age 16. A line fitted to the logarithms of their age frequencies shows a survival rate of about 81 % but the variation around this line is so great that its significance may be questionable.

The size limit imposed by law and the large-mesh trawls used by commercial fishermen apparently tend to preserve the males. Further information concerning

Figure 5. Number of tagged *Parophrys vetulus* released in the study area in September, October, and December, 1953.

survival rates is now being obtained from a study of comparative tag recoveries of males and females. Samples of *Parophrys vetulus* obtained periodically for the past two years form the basis for a study of age and growth of this species now in progress. Some indication is now at hand that an increase in growth rate has already occurred in Holmes Harbor following its opening to commercial fishing in January 1953. Further changes in growth will be watched with interest in future years.

**Tagging experiments.**

Pruter and Van Cleve (1954) described an exploratory tagging experiment that involved the release of 2741 tagged *Parophrys vetulus* in Holmes Harbor between 26. and 31. December 1952. Tags recovered during January and February 1953 showed a close relationship of the Holmes Harbor fish with those in neighbouring areas but lack of tag releases outside the harbor prevented accurate estimates of the size of the population or of mortality rates. The past year's programme was designed to overcome these deficiencies and 5034 tagged fish were released in areas 1—8 in two experiments (Figure 5): 3948 fish were released between 1. and 5. September 1953, and a second group of 1086 fish between 27. and 30. December 1953. In addition, 420 fish were released in area 10 on 15. October 1953.

Recoveries from all 1953 experiments totaled 949 fish by 15. February 1954, the last day of the current season. In addition, 161 tags released in the initial Holmes Harbor experiment in 1952 were recovered during the current season. The distribution of all recoveries from the study area and from neighbouring fishing grounds is compared with the distribution of fishing effort and catch in Figure 6. Recovery of two tags off the Washington coast, one from the 1952 experiment and one from the September 1953 experiment, and 2 tags in area 11 just south of the experimental area represents a total loss of less than 0·5 % of all tags recovered this season. It thus appears that we can consider this population as an almost independent unit. However, efforts will be continued to

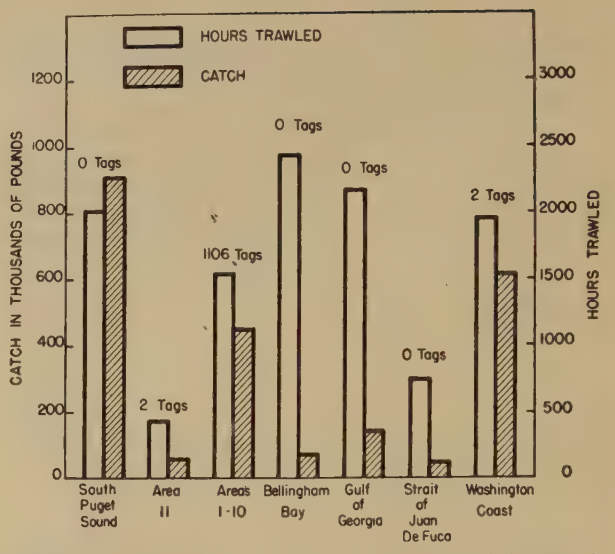


Figure 6. Comparison of the total number of hours of trawling and pounds of *Parophrys vetulus* caught in various areas with the number of tagged *Parophrys vetulus* caught in those areas.

recover all tags captured by fishermen in contiguous areas as well as in the study area.

The availability of tagged fish in Holmes Harbor varied widely during the fishing season of January and February 1953, leading us to suspect marked differences between the actions of tagged and untagged fish. Comparison of this year's Holmes Harbor recoveries from the 1952 experiment with those from the September 1953 tag releases indicates that the same type of variations in numbers of tagged fish caught per hour of trawling occurred in both (Figure 7). The cause can hardly be ascribed to differences in activity of tagged and untagged fish unless the effect of the tagging is still apparent a year after release. It could be considered as evidence of schooling. Since the fish that were tagged from each haul were released in one spot at the end of the haul in which they were captured, they may have remained in a school so that the fortuitous encounter by a trawl with a school of fish containing tagged members could have given the appearance of the variations noted. However, even this hypothesis cannot explain the correlation in rate of capture of tags from two experiments in which the tags were released almost one year apart. Since the use of tags to calculate population size or mortality rate assumes random sampling the use of tag recoveries from the experiments involved will require a sufficiently wide distribution of fishing to counterbalance the variations in distribution of tags. Care must be taken in such an analysis to use large enough subdivisions of the fishing season that randomness may be approximated in the sampling.

If sampling of tagged fish was sufficiently random to give usable results, the population of *Parophrys vetulus* for areas 1 to 8 can be calculated from the

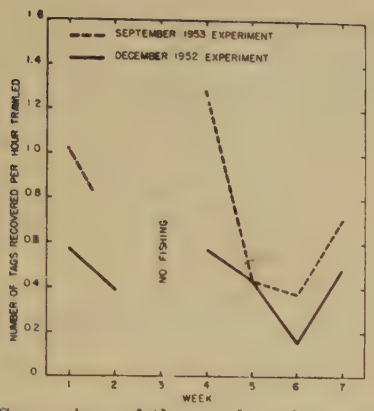


Figure 7. Comparison of the number of tagged *Parophrys vetulus* released in Holmes Harbor in December 1952 and September 1953 which were caught per hour of trawling in Holmes Harbor by weekly periods, 1. January—15. February 1954.

recoveries of tagged fish greater than 295 mm. in total length at tagging released in September 1953 and again from those recovered from the December 1953 releases. The first result which would correspond to an estimate of the population at the time of release in September was 821,000. Ninety-five percent. confidence limits (CHAPMAN, 1948) were estimated to be 736,000 and 922,000. The second estimate of the same population in December after a total of about 70,000 fish of commercial size had been taken was 650,000 (95 % confidence limits 548,000—780,000). The agreement between the population decline and size of catch is well within the limits of error. Areas 9 and 10 were excluded from these preliminary estimates because of the rather small exchange of tags between those areas and areas 1 to 8. However, it is interesting to note that an estimate of the total population in areas 1 to 10 from the September tags gave a total population of 2,560,000 fish. Total landings from all areas for the season amounted to about 518,000 fish, which would be a withdrawal of about 20·2 %. The fishing rate for Holmes Harbor for the previous season was about double this figure.

Total tag recoveries from all areas for the September 1953 experiment amounted to 16·7 % of releases while 12·8 % of the December tags were returned. In contrast, recoveries from the 420 tags released in area 10 alone amounted to 24·3 %. A study of the relationship of these recoveries to fishing pressure and total catch within the different areas is in progress to determine if they can be used with confidence to calculate population parameters.

**Relation of population and environment.**

Attempts to relate variations in populations with variations in environment require first a definition of what the environment encompasses. Predator-prey or food relationships have been treated on theoretical mathematical lines by LOTKA (1925), VOLTERRA (1928), and others, but the assumptions involved in their work are difficult to reconcile with conditions as they occur in nature. Simplification of conditions has again been carried too far in this field which in reality should involve a synthesis of information from all phases of the environment. The complications involved in such a synthesis make it impractical at present since most data that are now available have resulted from programmes of observation that were either not sufficiently complete or well enough coordinated to provide data that are comparable.

A start can be made by accepting the fact that a particular species of fish is in itself an inseparable part of its own environment. Further all species of fish living together in any area really form a population of greater complexity than that of a single species, but one which is inextricably bound with the fluctuations in abundance of its component species. It seems inconceivable that variations in the population size of one species can be independent of variations in numbers of other fish inhabiting the same area and either competing with it for food, furnishing part of its food supply, acting along with man as a predator, or just occupying space. Elucidation of all the complex interrelationships involved would be an ambitious undertaking indeed but it should be possible to follow variations in relative abundance of the different species if adequate sampling techniques can be developed.

Detailed population studies of 47 different species of fish (our species list is probably incomplete) would be impractical, but exploratory work in several directions is under way. Standardized hauls with the experimental vessel are being used to obtain periodic estimates of the relative abundance of different species in terms of trawl catches. Development of accurate records of commercial landings of all species, whether food fish or scrap fish, will be used to measure the productivity of each and of the area as a whole in terms of fish protein. Finally, if the abundance of other species can be related to the size of this intensively investigated *Parophrys vetulus* population, relative changes in the various segments of the fish population complex can possibly be evaluated.

In fulfilment of this objective, complete enumeration and weights of each species taken in experimental hauls by the research vessel are being accumulated. Landings of scrap fish as well as food fish by the commercial vessels are also being recorded and will be refined as the programme proceeds. Results are still in the realm of speculation while techniques of sampling and treatment of data for *Parophrys vetulus* are worked out. It is hoped that development of the mathematical concepts of so-called "population dynamics" will be possible as sounder foundations for basic assumptions and hypotheses are developed.

It is not expected that correlations between variations in hydrographic environment and fish populations can be intelligently investigated until the complex of what we may term the fish environment is better understood. When such correlations are attempted, hydrographic observations of both spatial and temporal detail at least comparable with our fishery observations will be required.

## 12.

# Information on Sampling and Working Methods in Market Investigations of the German Deep-Sea Fisheries.

*By* J. Lundbeck

An important part of the German sea fisheries is exercised in distant waters widely separated from each other. Therefore the observations and investigations on catching conditions must be done with the help of landings by commercial vessels. Only the methods in use to carry on such work are dealt with here.

**A. Fisheries statistics** under such circumstances are not only an indication of the size of the catches, but are actually the basis of the scientific work. Since about 1930 there has been undertaken a thorough analysis of the commercial landings as to species, market categories and size composition, place of capture, time of actual fishing and catch per unit of effort. In addition, since 1935 current statistics of such a kind have been compiled, which since 1939 and again since 1949—54 by stages have been combined with the official statistics.

The basic unit is the single trip, and because of the lack of book-keeping onboard the trawlers, the required information must be as simple as possible.

1. The places of capture are defined as rather large areas according to the usual fisherman's terms, as shown in Figure 1. The limits have been defined in such a way that each area is of a rather uniform and distinct biological character. But the area is still so large as to include essential differences in feature and composition of the catches. For example, off Iceland the fishery took place previously immediately outside the territorial limits, but now it operates on the edge of the shelf where wholly another stock of commercial fishes are met with. Therefore, if the catches have altered by quantity or composition, there is no evidence at all of any change in the basic conditions.

Apart from this the limits are of no importance anyway since the fishing fleet mostly aggregates in rather restricted localities and does not scatter very much to the outside. However, it has not been possible in all cases to maintain the limits set by ICES, due to the fact that in several cases important fishing places whose catches are registered as a whole, are lying on both sides of these limits.

2. The fishing day has been chosen as the time unit of fishing and for calculation of comparable yields. Here, too, the skippers or mates will be able to give information from immediate memory. There will no doubt be wider scope for inaccuracy and faults than for fishing hours. But in principle the days fishing are as correct an expression of the time spent in fishing as the hours. On the average both can be connected together. A calculation from the log books of nearly 5000 German trawler trips in 1930 averaged 15·1 days or 366 hours for one whole trip,

of which 6·8 days or 166 hours were for running from and back to the harbour,

of which 1·4 days or 32 hours were for gales and other loss of time,

of which 6·9 days or 168 hours were for fishing.

Each day therefore of 24 hours of real fishing (towing the net over the bottom) amounted to between 60 and 88 % of the total. This depends on the duration of the haul and the time necessary for shooting and hauling the trawl. But with the shorter hauls in deeper water this percentage recently has diminished, on the Norwegian coast, to 26—60 %. Also if trawling is only paying during day-time or at night, or if heavily variable catches need longer intermittent searching, that means reduction of productive fishing time. In the exceptional case of very short and very prolific hauls on the west coast of Greenland, the net was only 50 hours in action in the course of 8 fishing days.

3. The catch per fishing day then serves as the comparable unit of yield. It should refer to as narrow as possible an area in a space of time. In practice the data for the above mentioned catching places and every month are summed up. Only in special cases a subdivision into depth-zones, 5 or 10 days etc. can be undertaken. This calculation does not need complete statistics of the whole landings; on the contrary all doubtful information which originates from more than one place is left aside.

Figure 1. Division of fishing areas used in the German deep-sea fisheries statistics (some division lines discontinued for simplification or because of changes in the distribution of the fishing fleet are marked by hatched lines).

The fishing technique of the German deep-sea trawler fleet is so uniform that there are no difficulties in that direction. Only the differences in tonnage and engine power of the ships have an essential influence on the yield. Comparative calculations resulted in the following relations between average catch per day of the various size groups of vessels:—

| Gross tonnage m.³ | 400–600 | 600–800 | 800–1100 | 1100–1400 | 1400–2000 |
|---|---|---|---|---|---|
| In herring trawling ... | 76 | 100 | 140 | 172 | 175 |
| In northern waters.... | 83 | 100 | 151 | 181 | 238 |

The correlation of the unit yield with the horse powers, which increase according to the tonnage of the ships, is a similar one, but is not considered further.

From the size composition of the fishing fleet at work in the different areas there can be estimated, by what amount the yield should have been expected to increase in the course of several years. That has to be taken into consideration and to be compared with the yields actually obtained. This increase has been calculated, for instance, for the decennary 1925—1935 by about one third and almost equally for the years since 1946. In reality the increase has often been greater than expected from these calculations because of improvements other than the size of the ship and engine. And without doubt in some cases, probably for the Norwegian coast, an actual decrease in yield has been hidden by the increase in technical catching power.

**B. The commercial landings** depend as to quantity and composition on the place of origin, the species of fish occurring and their density, the intensity of fishing and its distribution in place and time, the selection for market purposes according to price and the wishes of the consumer and the subdivision into market categories. At any time the most favourable fishing localities and the market conditions are the most important factors for deciding which areas and species should be preferred. The fist two items are the object of the fisheries statistics treated above, whereas the last ones need further observations.

1. The catchable stock, i. e., the fish of such a size, that they are caught by the gear cannot be defined exactly because of the lack of information on the mesh selection. Only the slope of the size distribution curve

**Table 1.** **Average Sizes within the Market Catagories and whole**

| | | Market category I | | 50 % selection | | Market category II | | 50 % selection | |
|---|---|---|---|---|---|---|---|---|---|
| | | cm. | kg. | cm. | kg. | cm. | kg. | cm. | kg. |
| *Gadus callarias* | S | 83·0 | 4·94 | 73·8 | 3·7 | 63·7 | 2·23 | 59·5 | 1·9 |
| | N | 87·6 | 4·98 | 78·7 | 3·7 | 68·2 | 2·33 | 56·8 | 1·3 |
| *G. aeglefinus* | S | 59·9 | 1·69 | 56·5 | 1·46 | 51·7 | 1·05 | 52·3 | 1·18 |
| | N | 68·5 | 2·66 | 62·9 | 2·28 | 58·5 | 1·60 | 50·1 | 1·17 |
| *G. merlangus* | S | 42·0 | 0·56 | → | → | 32·8 | 0·26 | — | — |
| | N | — | — | — | — | — | — | — | — |
| *G. virens* | | 85·0 | 4·48 | 75·2 | 3·24 | 68·2 | 2·11 | 57·8 | 1·40 |
| *G. pollachius* | | 72·1 | 2·62 | 66·1 | 2·5 | 57·6 | 1·47 | — | — |
| *Molva molva* | | 105·4 | 5·69 | 70·5 | 1·7 | 57·7 | 1·11 | ← | |
| *M. byrkelange* | | 99·3 | 3·46 | 64·9 | 0·71 | 59·6 | 0·76 | — | — |
| *Merluccius merluccius* | | 88·4 | 3·43 | 82·7 | 3·8 | 70·3 | 2·02 | 68·1 | 2·2 |
| *Brosmius brosme* | | — | — | — | — | — | — | — | — |
| *Sebastes marinus* | | 45·2 | 1·35 | 36·5 | 0·72 | 35·8 | 0·62 | | |
| *S. viviparus* | | — | — | — | — | — | — | — | — |
| *Anarrhichas lupus + minor* | S | 69·2 | 2·71 | 61·1 | 1·81 | 47·7 | 0·93 | — | — |
| | N | 87·7 | 5·55 | 67·6 | 2·49 | 62·5 | 1·78 | — | — |
| *Lophius piscatorius* | | 95 | 4·1 | 68 | 3·3 | 64 | 3·0 | ← | |
| *Cyclopterus lumpus* | | — | — | — | — | — | — | — | — |
| *Trigla gurn. + Tr. corax.* | | occasionally category "large" mainly with *Tr. corax* | | | | | | | |
| *Trachinus draco* | | — | — | — | — | — | — | — | — |
| *Pleuronectes platessa* | S | 47·9 | 1·12 | 50·7 | 1·23 | 40·8 | 0·67 | 40·1 | 0·55 |
| | | market category: V: | | | | 23·2 | 0·13 | | |
| | N | market category I/II: | | | | 49·5 | 1·30 | 44·9 | 1·03 |
| *P. limanda* | | 31 | 0·29 | — | — | 24 | 0·15 | — | — |
| *P. flesus* | | 38·9 | 0·56 | 35·7 | 0·44 | 31·6 | 0·30 | 29·9 | 0·27 |
| *P. cynoglossus* | | 45·2 | 0·60 | 44·7 | 0·59 | 39·4 | 0·38 | 37·4 | 0·31 |
| *P. microcephalus* | | 37·9 | 0·56 | 35·0 | 0·49 | 30·6 | 0·32 | — | — |
| *Solea vulgaris* | | 35·5 | 0·39 | 36·0 | 0·44 | 30·2 | 0·24 | 30·0 | 0·24 |
| *Drepanopsetta plat.* | | — | — | — | — | — | — | — | — |
| *Lepidorhombus whiff.* | | 48·8 | 0·87 | 44·2 | 0·68 | 35·6 | 0·38 | — | — |
| *Hippoglossus hippoglossus* | | 176·8 | 38·5 | 117·5 | 18·2 | 82·5 | 6·14 | 73·1 | 3·7 |
| *Reinhardtius hippoglossus.* | | similar to the foregoing | | | | | | | |
| *Scophthalmus maxim.* | | 64·9 | 6·10 | 51·0 | 2·6 | 52·5 | 2·50 | 47·3 | 2·0 |
| *Rhombus laevis* | | 55·1 | 2·48 | 50·8 | 1·86 | 45·5 | 1·32 | 39·3 | 0·90 |
| *Scomber scombrus* | | 40 | 0·6 | 37 | 0·4 | 33 | 0·24 | ← | |
| *Orcynus thynnus* | | — | — | — | — | — | — | — | — |
| *Raja* spp. | | 104·9 | 5·67 | 92·0 | 4·39 | 84·6 | 3·20 | — | — |
| *Acanthias vulgaris* | | — | — | — | — | — | — | — | — |
| *Isurus cornubicus* | | — | — | — | — | — | — | — | — |

S = Southern region, mainly North Sea.
N = Northern regions.
An arrow means that one market category does not extend beyond the size range of the neighbouring one.
[1]) Averages for Iceland and Barents Sea separated.
[2]) Averages for each of the two species.

on the left of the position of maximum percentage can be determined.

2. The marketable stock, containing all fishes above minimum commercial size, is a selection of the catchable stock. It should be pointed out, that the market selection is highly relevant in fishery statistics used for biological purposes. It does not only influence the quantity of landings absolutely, but also the yield per unit of effort and the size composition of the landings. Unfortunately it is not easy to get information in that direction. In order to calculate the percentage retained and discarded in each size group, the composition of the catchable stock must be known. Only observers on board the trawlers can make estimations of the undersized fish for a single haul or a whole trip and measure adequate samples of them. Information, therefore, refers only to individual cases, and since there is very wide variation, often not more than an approximation can be reached.

3. The market categories are often used as a source of information as to the size composition of the different commercial fishes landed. But experience has shown such an irregularity both from economic and from biological causes that it is impossible to

**andings and average Sizes of 50 % Selection, 1929—1938.**

| Market category III | | 50 % selection | | Market category IV | | Whole landings | | 50 % mark. selection | |
|---|---|---|---|---|---|---|---|---|---|
| cm. | kg. | cm. | kg. | cm. | kg. | cm. | kg. | cm. | kg. |
| 41·0 | 0·62 | ← | — | 35·1 | 0·37 | 49·1 | 1·48 | 34·2 | 0·33 |
| 57·5 | 1·23 | | extra large: | 115 | 12 | 78·2 | 3·63 | 45·6 / 60·0 | 1·2 / 2·0[1]) |
| 43·5 | 0·66 | 43·5 | 0·67 | 38·1 | 0·43 | | | | |
| market category V: | | 37·6 | 0·43 | 29·6 | 0·19 | 30·5 | 0·23 | 22·5 | 0·10 |
| 47·6 | 0·92 | 40·1 | 0·58 | 39·5 | 0·49 | 58·5 | 1·82 | 38·3 / 42·2 | ·51 / 0·64[1]) |
| — | — | — | — | — | — | 33·7 | 0·29 | 23 | 0·08 |
| — | — | — | — | — | — | 46·4 | 0·80 | 45·0 | 0·69 |
| 50·6 | 1·18 | — | — | — | — | 80·9 | 3·91 | 45 | 0·8 |
| — | — | — | — | — | — | 65·5 | 2·02 | „ | „ |
| 55·8 | 0·84 | — | — | — | — | 94·3 | 4·52 | > 50 | 0·8 |
| — | — | — | — | — | — | 93·5 | 2·88 | > 60 | 0·7 |
| 51·1 | 0·92 | — | — | — | — | 58·0 | 1·26 | 35 | 0·3 |
| — | — | — | — | — | — | 59·6 | 2·02 | 40 | 0·7 |
| — | — | | extra large: | 70·4 | 5·12 | 41·2 | 1·28 | 32·4 | 0·54 |
| — | — | — | — | — | — | 25·8 | 0·31 | — | — |
| — | — | — | — | — | — | 62·0 | 1·73 | 38 | 0·4 |
| — | — | — | — | — | — | 70·5 + 89·6[2]) | 2·4 + 2·6[2]) | 50 | 1·0 |
| 44 | 1·0 | — | — | — | — | 79 | 3·8 | 40 | 0·8 |
| — | — | — | — | — | — | 44·0 | 2·61 | — | — |
| | | | | | | 28·3 | 0·20 | 20 | 0·08 |
| — | — | — | — | — | — | 26·3 | 0·11 | 20 | 0·08 |
| 33·7 | 0·38 | 33·7 | 0·35 | 26·5 | 0·20 | | | | |
| plaice mostly category IV: | | | | 25·9 | 0·16 | 27·8 | 0·21 | 24·5 | 0·14 |
| et category III/IV: | | | | 35·1 | 0·43 | 37·5 | 0·58 | 28 | 0·28 |
| — | — | — | — | — | — | 25·0 | 0·16 | 22 | 0·14 |
| 27·4 | 0·21 | — | — | — | — | 30·6 | 0·30 | 24 | 0·15 |
| 32·6 | 0·20 | — | — | — | — | 37·3 | 0·35 | 24 | 0·07 |
| — | — | — | — | — | — | 35·0 | 0·49 | 24 | 0·16 |
| 27·5 | 0·16 | 25·5 | 0·14 | 24·3 | 0·12 | 30·9 | 0·25 | 25 | 0·13 |
| — | — | — | — | — | — | 42·0 | 0·72 | 35 | 0·6 |
| — | — | — | — | — | — | 36·4 | 0·48 | 25 | 0·12 |
| 58·5 | 1·98 | 50·8 | 1·20 | 44·3 | 1·05 | 67·9 | 3·24 | 30 | 0·31 |
| | | | | | | 58·8 | 2·19 | „ | „ |
| 43·8 | 1·62 | 42·0 | 1·4 | 36·9 | 1·22 | | | | |
| market category V: | | 30·8 | 0·65 | 28·4 | 0·34) | 46·8 | 2·22 | 24 | 0·27 |
| 31·3 | 0·39 | 35·9 | 0·66 | 27 | 0·25 | | | | |
| market category V: | | ← | — | 23 | 0·15) | 40·8 | 0·78 | „ | „ |
| 28 | 0·13 | — | — | — | — | 32·2 | 0·26 | — | — |
| — | — | — | — | — | — | 261 | 230 | — | — |
| — | — | — | — | — | — | 90·6 | 3·78 | 50—75 | 0·9—2·5 |
| — | — | — | — | — | — | 67·4 | 0·86 | 40—60 | 0·17—0·6 |
| — | — | — | — | — | — | 217 | 80 | — | — |

define any category exactly. Of course, the composition of the whole catch as well as of each market category depends on the composition of the stocks themselves and their changes in place and time. Already onboard ship, pre-sorting takes account of the sale conditions to be expected. On the market too, sorting is not wholly uniform, in spite of several agreements on weight limits for each category. When compared with exact length compositions, the percentages of the market categories do not always show similar variations and differences.

In general the market categories correspond to the needs of the fishing industry. Their number has grown in the course of time, in some cases up to 5 or 6. The most exact sorting is done with highly valued species, for example sole; but it must not be forgotten that sorting is always by eye.

In recent years no thorough survey of market categories and selection has been undertaken, but unmistakable signs show that for some of the most important species the minimum marketable sizes are higher. Those for cod, coalfish and redfish have been fixed, by voluntary agreement, at 750, 1500 and 750 gr. respectively. This development is due partly to the greater requirements of the consumers, part y to the greater maintenance costs of the large trawlers and to the high prices of to-day.

Table 1 contains data on the market categories in use, giving the average sizes in the grand total and the 50 % selection points. The average sizes for the whole landings of each species and the 50 % points of market selection are included. This summary gives a general impression, but it has to be borne in mind that large deviations are common.

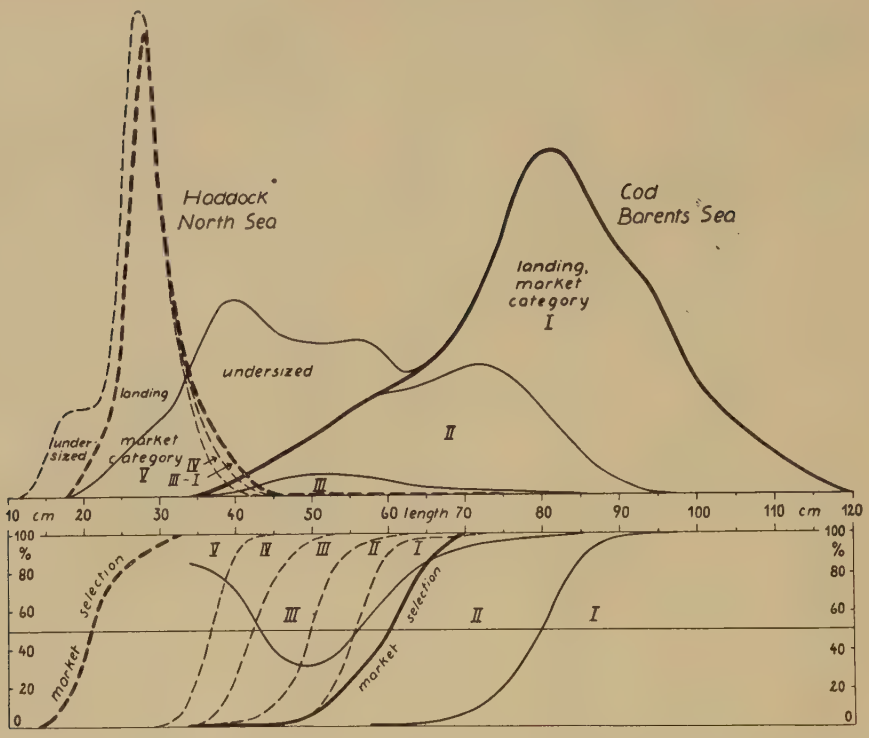


Figure 2. Two examples of market selection and sorting into market categories: the North Sea haddock (broken lines) and the cod from the Barents Sea (full lines). Curves of the size composition of the catch and the market landing, divided into market categories (above), the curves of the percentage distribution between the unmarketable and marketable fishes as well as between the market categories (below).

**C. The market investigations** have to take account of these circumstances. That means, only the selected market landings are available, and they are divided into size categories. The aim is to reconstruct the single landing and to gain an adequate representation of the total quantities landed by a number of single landings.

1. Samples shall in principle be typical of the catches from a distinct region and season. Mixed catches therefore cannot be used.

Single samples from catches in an unimportant fishery can be of worth only to enable special comparisons. The best way to represent large parts of the landings will be to take as many samples as possible from intensive fishings. Up to about 50 samples, including more than 10,000 individual fish, have been worked up together. But normally not more than 10 and often only a few samples must suffice. The material variation seems more important than the mathematical certainty of a single sample. Therefore it is thought more favourable to have a larger number of small samples than a small number of larger ones.

2. Length measurements, as the simplest means of analysis, are made in the first instance, partly by reading from a scale board, and partly by marking the length by an awl on a sheet of paper and tabulating afterwards. The lengths are grouped at whole centimetre intervals. In principle enough fish must be measured at a time, so that the whole length scale becomes sufficiently reliable. Their number therefore depends on the number of 1 cm.-intervals. Whereas in the beginning several hundred fishes were taken, later on they have been generally reduced to about one hundred. The random faults no doubt are then larger, but as mentioned above the greater number of samples to be handled is more valuable. Except for extreme cases no attempt has been made to measure a definite percentage of the fishes present.

Each market category has to be represented by a separate series of measurements. To reconstruct the whole catch, every series has to be converted to the total quantity of the respective market category on the base of known weights. Finally the calculated numbers of fishes within every single length group are summed giving the length composition of the whole catch. This forms the basic material for further treatment and consideration.

No attempt has been made to calculate deviations and errors; certainly the single sample does not correspond to the requirements of mathematical precision. Only the sum of a whole group can be used, as far as

average composition and the variability of the fishery in question are represented adequately. The reliability is best indicated by decreasing irregularities in the distribution to the single 1 cm.-intervals. But smoothing is necessary in almost all cases, and mostly the sums for 5 cm. of length are used.

3. The age composition is based on the length measurements, because the numbers of age determinations are much less than the length measurements. Generally some hundred or a few thousand data from one to about ten samples may be combined. In the first years only scales have been used, which can be taken from market fish without damaging them. But the difficulties in making an exact age determination of higher ages resulted in otoliths being used. At present these are obtained almost exclusively from the skeletons after filleting, from the heads or from whole fishes through the gill cavity.

Usually the number of year-classes within a space of 5 cm. (without respect to market categories) are converted to the percentage of the corresponding length group by measurements. In that manner the percentage age composition of the landings is immediately obtained. Also the absolute number of fish of each age-group or the average per fishing day is calculated for a fishery in a distinct season or region as well as for the whole year and area in order to know the practical importance of the year-classes.

Considering the taking of equal samples from several market categories, of which very different quantities are contained in a landing, it is not deemed practicable to calculate average lengths of the year-classes. No growth investigations therefore can be made on the basis of market investigations alone (except in special cases when sorting seems not to disturb the natural size composition of the stock fished). The conversion of age-groups from numbers as well as generally from lengths to weights is exercised by some 6000 statements of individual weights of all sizes of commercial species.

**D. In further treatment and utilization** of the market investigations, because of several shortcomings in the material, only the fishery and the landings can be taken as a basis for consideration. To what extent they give information on the natural stocks of fish is a question for further examination.

1. The total landings represent the total commercial output as well as the fishing mortality absolutely. In this latter respect, however, the discarded quantities of non-marketable fishes should be included. Samples of them can be obtained only by work at sea and therefore only in a few cases.

The total fishing intensity corresponding to the quantities caught is expressed adequately by the number of fishing days, which, if desired, could be connected internationally with the fishing hours of other countries. Whereas fishing intensity is meaningful only in respect to the whole area of distribution of a species or stock, the importance of distinct parts of this area to the fishery as shown by total landings may be of immediate interest.

2. The catch per unit time demands more thorough examination. The large number of commercial vessels at work secure a rather exact average calculation. But it has been experienced that in an unfavourable fishery a shortening of the season or a restriction to a narrow area of good catches with participation of only a small part of the fleet may result in much higher average unit yields than would have been calculated for a full fishery during the whole season. Especially in the Barents Sea near the outer limits of distribution and migration of cod and haddock there may occur a real reversal: with the rising temperature in the hydrographical spring the shoals remain concentrated for some time and may give single high yields; later on in hydrographical summer the warm water allows a scattering of large quantities of immigrants with only smaller catches over the whole area; finally the decreasing temperature in early winter again sweeps the fishes together giving increased catches at distinct points. For this reason also, years of below-average heating in spite of weak immigration show higher average unit yields than warmer years.

Generally speaking the yield per unit time depends not only on the total stock present but also, and often primarily on ecological influences by their effect on the strength and regularity of the aggregations of commercial fishes as well as from the experience and ability of the fisherman to discover the most favourable catching possibilities at any time.

3. As to length and age composition it may be repeated that market selection should be considered as far more relevant than the market categories, and that to take account of the material differences is more important than the deviations by mathematical chance. Attempts have been made to calculate, instead of percentages, the absolute quantities of fish in each length and age-group, but mostly strong and irregular differences seem to make that unpracticable, for instance in the North-Eastern Area. Only when taken in the grand total do the length and age compositions become more regular in spite of their dependance on the distribution of the fishery in space and time. For the same reasons mortality and similar rates have not been calculated.

4. Finally the relations to population studies may be mentioned. From the foregoing such relations cannot be thought to be very simple or immediate. But in most cases no other and better information for the natural population of commercial fish is available.

A certain independence from the commercial fishery can be obtained by using the catch per unit time calculated not from the bulk of landings, but for single groups equally distributed over the area or the season in question and summarized as a simple mean value. That would often be a way to approach at least some conceptions on the populations or make possible comparisons without reference to intensity, location, and course in time of the fishery. But here the final limits of evaluation from market investiga-

tions without additions by further research work begin to be felt.

In considering the success of the commercial fishery generally we have to deal with two causes: firstly the absolute number of fishes present, which is dependent on fluctuations in year-classes; secondly their distribution and movements. Only the first item can be fully taken into consideration. The second one at present leaves still too many open questions of a general biological kind. In future work perhaps two points could be taken more into consideration: availability and behaviour. Because of the restriction of the fishery to such regions and times as are expected to give paying catches practically the availability is limited from economic regards. Behaviour should be understood not only in the sense of extended migrations in vertical and horizontal directions, but also in single features to be read from echo-sounding etc. Thus availability, arising from economic and technical as well as from physiological and ecological factors would have to be taken into account for its immediate practical effect and as a biological factor for stock maintenance.

## 13.

# Méthode d'Echantillonage de Harengs en Belgique.

*Par* Ch. Gilis

Les concentrations de harengs de la Mer du Nord, dont l'exploitation constitue une pêcherie très importante pour les pêcheurs belges, font l'objet d'une étude approfondie à l'Institut d'Etudes Maritimes d'Ostende.

C'est depuis le Fladen jusque dans la Manche Orientale que les pêcheurs belges exploitent ces concentrations.

Leur étude est scindée en deux:—

1) celle du hareng dit "plein", pêché de Juillet à Octobre dans les régions septentrionale, centrale et méridionale de la Mer du Nord et

2) celle du hareng dit "guai" dans la mer côtière entre Ostende et Boulogne.

Les échantillons de harengs pleins sont récoltés par les patrons des harenguiers sur le lieu de pêche et généralement d'une des dernières pêches du voyage. A cet effet, on embarque un récipient en tôle galvanisée, pourvu d'un couvercle. Le récipient contient $\pm$ 100 harengs. L'échantillon est pris au hasard d'une pêche au moment même qu'elle est déversée sur le pont du navire et mis directement dans le récipient qui est conservé dans la cale à poissons jusqu'au débarquement de la pêche. Un membre du personnel de l'Institut d'Etudes Maritimes d'Ostende prend livraison du récipient et prend note de tous les renseignements utiles sur la pêche: lieu, date, nombre d'heures de pêche effectives, quantité pêchée, force motrice, etc.

Normalement on prend un échantillon par semaine, soit 400 à 500 harengs par mois; comme la saison du hareng plein dure 3 à 4 mois, le nombre d'individus examinés atteint $\pm$ 1,400.

Les échantillons de harengs guais sont récoltés par un membre du personnel de l'Institut dans la minque même au moment du débarquement de la pêche. C'est au hasard que le hareng est pris et mis dans un récipient analogue à celui décrit plus haut. Un voyage pour le hareng guai dépasse rarement les 24 heures; le poisson est conservé à frais sans glace.

Comme pour le hareng plein on étudie un échantillon par semaine. Comme la saison de la pêche de harengs guais dure 3 mois, le nombre de harengs guais examinés monte à $\pm$ 1,200.

Les harengs sont examinés aux points de vues de: longueur, poids, sexe, maturité, graisse mésentérique, âge, vertèbres, écailles en carêne ($K_2$) et contenu stomacal.

## 14.

# The English Fish Sampling Programme.

*By* A. C. Burd and J. A. Gulland

## 1. The Demersal Species.

**Sampling of the commercial catches.**

Samples of six species of demersal fish: cod, haddock, whiting, hake, sole, and plaice, are taken for length measurements at English ports. Samples of cod and plaice are also taken for age determination. All the length measurements are taken on the market directly after the fish are landed, and before they are sold by auction. The whole catch of each ship is then available, and any division of the catch by size or condition may be seen, and their quantities determined. The sampling unit used is one ship's catch, each sample consisting of measurements from all the sub-divisions of the catch. In addition to the actual number of fish measured at each length within each sub-division (recorded to the centimetre below), a record is kept of the weight of fish landed in every sub-division, whether by size or condition, the name of the ship, type of gear, date of landing, position of fishing, and time spent fishing. Those data are worked up to give the total numbers landed and the numbers landed per unit effort in each length group and where possible, age-group. Results for North Sea plaice have been published repeatedly in the *Annales Biologiques*.

Samples of **cod from the distant water grounds**, i. e., Greenland, Iceland, Norway coast, Bear Island, etc., are taken at Grimsby and Hull. The target figures are 5,000 fish measured (abt. 25 samples) each month at Grimsby, and 6,000 (abt. 30 samples) at Hull. The bulk of the measurements are done on fish from the Arcto-Norwegian stock, but samples (started recently) are also taken from Iceland and Greenland, particularly when the landings from these regions are heavy. At both ports the bulked and shelved fish are kept separately, and in addition each of these divisions is divided into two or three size categories, though these are generally ill defined. Each sample consists of one or more complete ten-stone boxes from each of the six or so categories. Their length composition is then raised to give that of each category, and hence the length composition of the whole ship's catch. This is then raised to give the catch at each port from each area each month, and finally the total catch at each port for the month and year.

Each month about 400 fin rays, in batches of 10—20, are taken for age determination. They do not form a completely random sample, but are chosen to cover all sizes of fish commonly occurring in the catches. These will be used to form an age/length key, and hence transform the length composition into an age composition (see Gulland, 1955).

Length samples of **North Sea cod** are taken regularly at North Shields. About 4,000 fish (20 samples) are measured each month. The fish are normally sorted into four categories: large, medium, selected small, and small, with further sub-divisions of the category large during the spawning season, when many fish of this category are landed. Each sample consists of one or more complete six-stone boxes, and the subsequent treatment is the same as for the distant water cod.

600 **haddock** (4 samples) are measured each month from North Sea trawlers at Grimsby. The landings may be divided into one to three categories, and a sample consists of a ten-stone box of each category landed. This sampling is done in cooperation with the Marine Laboratory, Aberdeen, and the length measurements are analysed further there.

Since early in 1954, regular length measurements of **whiting** have been made at Lowestoft, each month some 1,200 fish (8 samples) have been measured. No sorting is done for this species, and each sample consists of 100—150 fish from a ten-stone box. As this

is rather less than half a complete box, care is taken to sample from only one side of the box. This means that the sample consists of all fish originally on that side, and leaves very little opportunity for personal selection. To determine what fraction of the box, and hence of the total catch, has been measured, the rest of the fish in the box, which are not measured, are counted.

**Hake** measurements are made at both the important west coast ports; 3,000 fish a month (4—5 samples) at Milford Haven, and 4,000 (20 samples) at Fleetwood. Sorting by size is important at both ports, particularly at Milford Haven. There the categories are: large, medium, inters, small and needles, plus three categories of poor quality or damaged fish. At least one complete box of each of these categories is measured. These length compositions are then raised to obtain the length composition of the catch of each category. These are then combined for all samples in each quarter, to give the average length composition of each category. This is then used to give the catch from each area, and the total port catch, for each quarter.

At Fleetwood there are only three or four size categories: large, medium, sometimes selected small, and small, and one category of damaged fish. One or more boxes of each of these categories is measured in each sample; the subsequent analysis is the same as for Milford Haven. It has so far been impracticable to take regular samples of hake for age determination.

The most intensively sampled fish at English ports is the **plaice**. 10,000 fish (40 samples) are measured at Lowestoft each month, and 3,000 (10—12 samples) at Grimsby. At Lowestoft the sorting into size categories is very regular, three main categories being used: large, medium and small, plus one or two categories of poor quality fish. In each sample a complete ten-stone box of large fish is measured, and 75 fish each from a box of medium and small. As for the whiting, when not all the fish from one box are measured, care is taken to measure only from one side of the box, and to eliminate any possible personal selection. In half the samples the rest of the fish in the box are counted. In the other samples the number of fish in the box is calculated from the average size of the measured fish, using the relation between average size, and number of fish given by the first samples. About 50 fish from a box of rough or thin fish are also measured. The subsequent analysis to give the port's landings for each month is similar to that for hake. The sorting at Grimsby is less consistent than at Lowestoft, there usually being three size categories, but sometimes less. Each sample consists of a complete ten-stone box of large, and about 100 fish each from a box of medium and small; the usual precaution against personal selection is taken. The subsequent analysis to give the landings at the port each month are the same as for cod.

At each port 150 otoliths are collected monthly for age determination. These are selected so as to give 30 age determinations in the commonest 5 cm. length groups, and 20 in the others. This is therefore far from being a random sample, but is used to construct an age/length key. This enables the length distribution for each port to be converted into an age distribution.

Each month 2,500—3,000 **soles** (12 samples) are measured at Lowestoft. A sample is made up of a complete ten-stone box of large, and 100 fish out of a box of small, these being the only two categories landed. Once a quarter a sample of some 50 fish is taken for examination of otoliths and vertebrae for age determination.

As far as possible the estimates obtained are free from bias, but they can only properly refer to the ports, areas, and methods of capture from which the samples were taken. For instance, in the North Sea, the only cod samples come from trawlers landing at North Shields. Considerable quantities of cod are also landed at Grimsby and Lowestoft, whose ships, particularly from Lowestoft, fish distinctly different areas, and hence these fish are likely to have a different age and length composition to that of the samples. Again, plaice measurements are only taken from trawlers, though the landings from seiners make up an increasingly important fraction of the total English North Sea plaice landings. These may possibly have a different composition to trawlers, so that the samples may not be typical of the total English landings. However, the sampling programme does cover a considerable part of the species, areas and ports of the English fishery, particularly those for which population studies, and hence age and length compositions, are likely to be of major importance.

The exact magnitudes of the variances of the considerable number of estimates, obtainable from the above sampling, have only been calculated for the Lowestoft plaice landings. The coefficient of variation of the numbers in each age-group landed each year changes from about 4—10 % for the commoner III to VII age-groups, up to about 15 % for the age-groups VIII to XI.

The estimated numbers landed in each 5 cm. length group each month have coefficients of variation varying from under 5 % for the smaller groups, to some 10 % for the 50—54 cm. length group. The variances for other fish can be gauged by comparison with the Lowestoft figures. The determining factors are, firstly the number of samples, and secondly the degree of variation between samples, either for the complete catch or for the individual categories, when the method of working up takes into account the landings at the port in each category separately, e. g., for the hake and Lowestoft plaice. The latter is probably about the same at Fleetwood, for the hake, as at Lowestoft, and possibly rather less at Milford Haven. At the other ports, where the sorting is more erratic, and so cannot be used as a rough guide to the length composition of ships whose catch has not been sampled, the difference between samples is considerably bigger. This suggests that the estimates of the numbers landed in each length group in each year are, for the hake, probably within 5—10 % of the true value, but are not so accurately known for the other species.

**Sampling at sea.**

**North Sea.** A regular line of trawling stations across the southern North Sea is carried out in January, April, July, and October in co-operation with Dutch investigators. Ten stations are regularly worked by R. V. "Sir Lancelot", and the two inshore stations by the Dutch research vessel. This programme is designed to obtain information on the abundance, growth and distribution of the younger plaice (less than 4 years old) which are not represented in the commercial catches.

A one-hour tow with the small Dutch trawl is made at each station. The weight of each species caught is recorded and when possible all plaice, dab, whiting, sole, brill, and turbot are measured; plaice to the mm. below, the rest to the cm. below. The otoliths of plaice and sole are also taken. When catches are heavy only a sub-sample is taken of the plaice, dab, and whiting catch. For plaice, a sub-sample consists of at least 200 fish otolithed, and a basket measured; for dab and whiting some 200 fish of each species are measured.

When a sub-sample is taken, the whole catch is picked up and weighed, and divided, a few fish at a time, among as many baskets as the denominator of the fraction required, e. g., if required to sample one-quarter of the catch, 4 baskets are set out, and the catch divided among them. One basket is then taken as the sub-sample.

**Arctic.** Since 1949, R. V. "Ernest Holt" has been working regularly throughout the year in the Arctic, and a large number of trawl hauls have been made. However, the area covered during any period has of necessity been only a small part of that of the whole cod stock, so that the catches cannot be used as a measure of total abundance. The trawl has mainly been used as a sampling instrument to map the distribution of fish within a relatively small area, in relation to environmental factors, chiefly temperature. Length sampling of the catch is aimed at giving a rough qualitative picture of the fish in the area. Otoliths and fin rays are taken for investigations on age determination, partly to establish whether the fin ray may be used for age determination of the commercial landings, and hence ultimately to obtain indices of abundance of year-classes and estimates of mortality. Otolith samples are also used to give a picture of length at age, and hence growth rate. Detailed examination of the otolith is used to discriminate between different sections of the cod stock.

As the objectives of the sampling of the catch are mainly qualitative, the demands for accuracy and lack of bias are less. The actual procedure in taking a sample is, when possible, to measure the entire catch. In heavy fishing the length sample is taken by standing in the pounds and measuring all fish within reach, in total at least 100. The otolith samples are usually of 50 fish taken "randomly", that is, with no deliberate selection, but with no particular care to avoid unconscious selection. It is therefore quite possible, but for the purposes required unimportant, that the otolith sample is not altogether typical of the catch. The total number of fish measured has varied between 2,500 and 7,000 a year, and the number of otolithed between 1,000 and nearly 4,000 in one year, the latter including 1,500 on one cruise.

J. A. Gulland.

## II. The Herring Sampling.

In the previous section by Gulland on the sampling of the demersal stocks landed at the English ports the stress is laid upon sampling in a manner such that the population parameters may be calculated. Before one can obtain useful mortality rates, etc., it is necessary to know whether the stock dealt with is homogeneous or a mixture of two or more different stocks. In the case of the North Sea demersal fishes the former seems to be true and the problem of sampling the fishery becomes one for obtaining the best estimate of the population parameters. However, the problem in working on the herring population is primarily in the identity of the stocks or "races". Only when the relationships between these stocks or "races" have been established will one be able to make reliable estimates of the fishing rates and mortalities.

Therefore in the English herring programme the stress is laid on the collection of scales and otoliths for age and racial analysis, with market measurements forming a lesser part of the work. This is in contrast to the demersal fish where the stress is laid on extensive length measurements on the market together with relatively small samples of otoliths for the construction of the "key" for conversion of the length data to age composition.

**Laboratory samples.**

Samples of herring are obtained from the three main fisheries on the English east coast, viz., the drift-net fisheries of East Anglia and North Shields and the ring-net/drift-net fishery off the Yorkshire coast which is centred on Whitby. The taking of these samples is essentially the same in the three localities. In East Anglia, four times a week throughout the season, a quarter-cran box of herring is bought on the market directly from a drifter. The drifter's position of shooting and total catch is recorded. At North Shields the unit is one-sixth cran and two or three samples are taken per week. At Whitby, which has been mainly a ring-net fishery, about three quarter-cran boxes are taken per week.

From the sampling unit 100 fish are taken for racial analysis. It is extremely important that there should be no selection in the taking of these fish and that the sample of 100 fish is truly representative of the fish in the box and hence of the catch of the drifter

**Table 1.**
**Mean Lengths, and their Differences, of the Scaled Sample and the Rest of the Box in a Series of $^1/_4$ Cran Samples of Herring from Lowestoft Market 1953.**

| Sample No. | Mean of: Sample (100 fish) | Rest of box | (S—B) Difference | Mean difference |
|---|---|---|---|---|
| 1..... | 25·49 | 24·96 (164) | + 0·53 | .. |
| 2..... | 25·55 | 25·02 (190) | + 0·53 | + 0·50 |
| 3..... | 26·05 | 25·57 (194) | + 0·48 | .. |
| 4..... | 24·95 | 24·65 (206) | + 0·30 | .. |
| 5..... | 25·37 | 24·71 (198) | + 0·66 | .. |
| 6..... | 24·81 | 24·76 (207) | + 0·05 | .. |
| 7..... | 25·83 | 25·12 (189) | + 0·71 | .. |
| 8..... | 24·26 | 24·34 (250) | — 0·08 | + 0·21 |
| 9..... | 25·56 | 25·39 (184) | + 0·17 | .. |
| 10..... | 26·19 | 25·99 (158) | + 0·20 | .. |

or ringer concerned. This is particularly important in cases of ports at which no length measurements are taken. Where length measurements are made one is able to construct a key so converting the length data into age compositions. If fish are taken from the box haphazardly, then there are several errors which may arise. Firstly, in cases where there is a big spread of lengths in a box it may happen that the large fish are found on the top of the box, the small fish slipping to the bottom. This may be overcome by dividing the box vertically with a board and taking all fish from one half first. As an example of this type of selection the mean lengths of the scaled sample and the rest of the box (number in brackets) are given above for a series of samples taken at Lowestoft. The top five pairs were taken straight from the box, the bottom half of the table by taking from half the box divided by a board.

The increased accuracy is obvious. However, a second feature derives from this table. In the case of Sample 7 it is seen that the scaled sample, despite the precautions taken, is as bad as those above. This type of discrepancy is usually accountable for by the rejection of fish with few or no scales suitable for age determination. In catches of young or spent fish this is often the case, especially with drift-net caught fish. Young fish and spents mesh, in the drift-net, further up the body than a full or adult herring and on being shaken out lose many of their scales. This source of error occurs frequently in the Shields fishery which is conducted mainly on the younger age-groups. Table 2 gives some idea of the extent of the errors involved.

This type of error is not only present in sampling from drift-net catches but also in sampling trawled herring.

To summarize, it has been shown that the taking of herring for scale samples usually results in the selection of the bigger fish and hence also the older fish. If sampling in this manner is alone used then the resulting age compositions will be biased in favour of the older fish and the younger ones will be under-

**Table 2.**
**Mean Lengths, and their Differences, of a Series of $^1/_6$ Cran Samples from North Shields 1954, showing Selection.**

| Sample No. | Mean of: Sample (100 fish) | Rest of Box | (S—B) Difference |
|---|---|---|---|
| 1..... | 24·87 | 24·36 (185) | + 0·51 |
| 2..... | 25·13 | 24·30 (164) | + 0·83 |
| 3..... | 24·36 | 23·87 (105) | + 0·89 |
| 4..... | 25·16 | 24·27 (94) | + 0·89 |
| 5..... | 24·56 | 23·24 (67) | + 1·32 |
| 6..... | 28·25 | 27·68 (87) | + 0·57 |

estimated. It is therefore the practice to obtain as representative a scale sample as possible and to measure the whole of the box. The "true" age composition of the box is then obtained by raising the total length measurements.

Extensive length measurements are taken at kippering and curing houses at Lowestoft and Yarmouth during the East Anglian season and on the market at Whitby. Very few measurements are made at North Shields where the object of the work is mainly for racial analysis. Thus using the scale samples for the construction of a key the age compositions of the catch in East Anglia and Whitby is known. The method used in East Anglia for the use of the age/length key to the total catch and the calculation of average numbers of each age-group landed per period are explained fully in Hodgson (1939).

**Collection of market statistics.**

The position of shooting and the amount of the catch is obtained from each drifter working at North Shields, Yarmouth and Lowestoft throughout the season. At Whitby, which has been mainly a ring-net fishery, the following statistics are collected:—

1) Total catch.
2) Number of "rings" made.
3) Catch per ring made.
4) Position of each shot.
5) Position and catch of some of the drifters is also recorded.

In the case of the drifters the catch per shot, which gives the apparent abundance of herring on the grounds, can be plotted in statistical areas. At North Shields these are sub-divisions of the statistical rectangles; the unit being one-ninth of the statistical rectangle as has been used in the charts recently published by the Dutch and Scottish workers. Similar charts of catch per shot and number of shots will be published for the North Shields fishery shortly. In East Anglia the catches per shot are plotted in areas one-eighteenth of a statistical rectangle.

However, the amount of confidence to be placed in these indices of abundance is subject to great doubt. Little is known of the behaviour of herring to drift-nets and of the effect of interference between one drifter's nets and the next on their ability to

catch herring. Also, different drifters may use varying numbers of nets each night. Thus the same catch per shot by an East Anglian drifter using 80 nets would represent a different abundance to that of the same catch by a small Scottish drifter shooting only 60 nets. The effects of tide and wind may cause the drifter to lie in a position in which the nets do not fish efficiently. Thus the apparent abundance of herring on one ground, expressed by catch per shot, may bear little relation to the true abundance. This is particularly applicable to the post-war years when the fleet has been reduced to about one-third of that in the thirties. In pre-war years the immense effort gave a better indication of abundance on the grounds.

The statistical areas used at Whitby for the ring-net fleet are 1 mile $\times$ 2 miles. At first sight this fishery would seem to be less liable to some of these errors and that a better estimate of abundance would result. The action of a ring-net is actively to catch a shoal as opposed to the inactive method of drifting, where the initiative is with the herring. However, such factors as the height of the shoals off the bottom, which governs whether the fish are catchable or not, and the engine noise and number of ships which act as scaring stimuli, are factors in this fishery which may and probably do give misleading indices of abundance when only catch per shot is known.

In summary, although statistics of catch and effort are known, the expression of a comparative catch per effort which is in relation to the true abundance is yet to be attained.

**Racial analysis.**

As was noted in the introduction one of the main problems of the herring fisheries is the interrelation between stocks. Trans-North Sea migrations of individual herring have been recorded by means of tagging, and fish tagged in the northern North Sea have been recovered in the southern North Sea and *vice versa*. In addition from scale studies it has been shown that in the East Anglian fishery fish resultant from autumn, winter and summer spawnings occur in varying proportions each year. At North Shields, which is a feeding area, the fish on the grounds vary rapidly in their racial composition. Similar features have been noted in the Yorkshire coast fishery.

Thus only very rough and approximate estimates of the population parameters can be made until the problems of the interrelation of stocks and the others indicated in the previous sections have been adequately answered.

A. C. Burd.

## 15.

# Outline of Sampling Methods used in Scottish Fish Population Studies.

*By* B. B. Parrish

Sampling programmes designed to furnish long-term data for dynamical fish population studies are being conducted in Scotland on the following stocks of fish:—

(1) Haddock: Faroe and North Sea.
(2) Herring: northern North Sea.

In the following sections brief descriptions of the sampling methods at present in use for each of these species are given in order that other workers may compare the published Scottish data with their own.

### Haddock.

#### (i) Faroe.

Detailed investigations of the population dynamics of the haddock stock at Faroe were commenced in 1950. These investigations are designed to provide annual estimates of the main population parameters, recruitment, growth, and the mortalities due to fishing and natural causes.

Three sources of sample data are utilized, (a) the steam trawler landings at Aberdeen (the Scottish fishery), (b) market landings at Grimsby (the English fishery, for which length measurements of the haddock landings are kindly supplied by the staff of the Ministry of Agriculture and Fisheries), and (c) research vessel trawling surveys. Source (a) provides most of the data used in population estimations, sources (b) and (c) providing supplementary material to test the representativeness of the Aberdeen data and to provide biological material usually unobtainable from market landings.

*Gear used in Scottish Fishery.* 30 ft. and 48 ft.[1]) otter trawls with V. D. modification. Cod-end mesh size in use not exceeding 100 mm. (stretched). Most of the trawlers 200 to 300 gross tons.

*Size categorization.* At present haddock are landed on the fish market in boxes, each weighing 8 stones, in three size categories, large, medium, and small.

*Sub-sampling methods.* Sampling is performed once weekly. A vessel is selected at random from the Faroe fleet and one box from each size category, also chosen at random, is sampled completely. All haddock in each box are measured to the nearest centimetre (tip of snout to extremity of caudal fin when the two lobes are held in the median line), and scales are taken from each fish for age analysis. The number of boxes of each size category landed by the sampled vessel, its trawling grounds and the number of hours fished are also recorded. In addition, statistics of the ground fished, the numbers of hours fishing and the quantities of each size category of each vessel landing every day are obtained subsequently from records collected by the staff of the Aberdeen Fishery Office.

#### (ii) North Sea.

Population data of the North Sea haddock stock have been collected for a large number of years by research vessel trawling surveys, and this constitutes the major source of North Sea haddock data at the present time.

*Gear used.* 30 ft. otter trawl with 20 ft. legs. Cod-end mesh size 80 mm. (stretched). A small-meshed bag completely covers the upper surface of the cod-end. Sampling vessel, F. R. S. "Explorer".

*Treatment of fish.* In routine trawling surveys, hauls of one hour's duration are conducted at each sampling position. (In some recent surveys half-hour hauls have been made.) All haddock taken in the cod-end and small-meshed cover in each haul are measured to the nearest centimetre, and scales are collected for subsequent age determination. Sub-sampling methods

[1]) This method of specifying the net is based on the length of the groundrope between tip of wing and bosum. The 30 ft. net, with a 20 ft. bosum, has a total groundrope length of $30 + 20 + 30 = 80$ ft., and a headline length of 62 ft. Corresponding dimensions for the 48 ft. net are 116 ft. and 90 ft. respectively.

are employed only when hauls are too large for all haddock to be handled, and whenever possible, sub-sampling is restricted to the small-meshed cover catch because of its smaller range of sizes (and ages). A satisfactory sub-sampling method for these small sizes is to select one or more baskets at random from a series filled by scoop from the deck pounds.

Detailed statistics of haddock catch and effort (hours fishing) for all British steam trawlers, for use in population studies along with these data, are provided by the Ministry of Agriculture and Fisheries and the Scottish Home Department. These give the total weight of haddock landed and the total number of hours fishing by British trawlers in each statistical rectangle each month.

## Herring.

Detailed sampling programmes designed to study the population dynamics of the herring stocks fished by the Scottish drift-net fleets in the North Sea were initiated in 1951, following the introduction of more detailed herring statistics collection at the main herring ports.

The sources of population data are the commercial drift-net fisheries, operating from local ports. Sampling is conducted at each of the three ports, Fraserburgh, Peterhead, and Lerwick throughout the duration of the summer fishery.

*Gear used.* Fishing from these ports is entirely by drift-nets, with mesh sizes ranging between 32—36 rows per yard. The mean mesh size is rather higher in the Shetland fishery from Lerwick than in the north-east coast fishery. The dimensions of the net, as normally used, are: length = 100 ft. approximately, depth = 45 ft. approximately.

*Method of sampling.* Fifty herring are selected at random from a vessel, also selected at random, on each day during the fishing season, at each of the ports (giving a weekly sample of 250 fish at each port). Experiment has shown that 50 herring taken at random from the top of the unsorted catch in the ship's hold provides a reasonably representative sample of the catch of that vessel. The fresh weight of each daily sample is recorded, and the sample is then placed temporarily in cold store at the port, prior to despatch to the laboratory. Length observations taken before and after storage show no significant change in mean length after the first day's storage. During the first day, however, a mean decrease in length of 3—5 mm. has been observed between fresh and stored herring in the length range 22—28 cm. Each herring in each daily sample is weighed to the nearest gramme, and is measured to the nearest millimetre[1]) (tip of snout to end of caudal fin when both lobes are held in the median line). Scales and/or otoliths are taken from all fish for age and "type" analysis, and records are taken of sex, maturity stage, intestinal fat, and vertebral number.

Records of the quantity of herring caught (in crans), the position of fishing, the duration of haul, and the number of nets shot are taken by statistics collectors (employed by the Scottish Home Department) for each haul made by each vessel (including the sampled vessel) landing each day at the three ports.

*Treatment of data.* The total number of herring landed at each port during any period of time is estimated from the values of (a) total catch in crans, and (b) average weight of herring sample as follows:—

Standard weight equivalent of 1 cran = 3·5 cwt. = 392 lb.
Average weight of herring sample = $x$ lbs.
Total quantity of herring caught = $Y$ lbs.
Then total number of herring caught = $\frac{19600\,Y}{x}$

(Periodic checks on these estimates are obtained from counts made by the staff of the Herring Industry Board.)

An index of abundance (catch per net-haul) is then obtained by dividing the estimated total number of herring caught in the required period, by the product of the total number of nets shot and hauls made by the fleet in that period.

Thus, average catch per net-haul = $\frac{19600\ Y}{x\ a\ b}$

where $a$ = number of hauls, $b$ = total number of nets shot.

Weekly or monthly indices of abundance of each age-group in the stock are then obtained by multiplying this figure by the proportion of each age-group in the total weekly or monthly sample.[2])

[1]) Scottish length data published in *Annales Biologiques* are the "after storage" lengths, which are grouped in centimetre intervals.

[2]) The indices of abundance for the constituent age-groups, estimated in this manner, are subject to a small bias due to the difference in weight between herring at different ages.

## List of References.


ANON., 1954: "Regulations and investigations of the Pacific halibut fishery in 1953". Rep. Internat. Pacif. Halibut Comm., 21, pp. 1—22.

ARMITAGE, P., 1947: "A comparison of stratified with unrestricted random sampling from a finite population". Biometrika, **34**, pp. 273—80.

BARANOV, F. I., 1918: "On the question of the biological basis of fisheries". Proc. Inst. Icht. Invest., **1**, 1, pp. 81—128.

BARNES, H. & BAGENAL, T. B., 1951: "A statistical study of variability in catches obtained by short repeated trawls taken over an inshore ground". Journ. Mar. Biol. Assoc. U.K., **29**, 3, pp. 639—60.

BARNES, H. & MARSHALL, S. M., 1951: "On the variability of replicate plankton samples and some applications of 'contagious' series to the statistical distribution of catches over restricted periods". Ibid., **30**, 2, pp. 233—64.

BARTLETT, M. S., 1947: "The use of transformations". Biometrics, **3**, pp. 39—52.

v. BERTALANFFY, L., 1938: "A quantitative theory of organic growth". Human Biol., **10**, 2, pp. 181—213.

BEVERTON, R. J. H., 1950: "The state of the southern North Sea plaice population during the years 1948 and 1949". Cons. Internat. Explor. Mer, Ann. Biol., **6**, pp. 133—4.

— 1953: "Some observations on the principles of fishery regulations". Journ. du Cons., **19**, 1, pp. 56—68.

— 1954: "A method of estimating mortality rates from war-time changes in abundance and structure of fish populations". Unpubl. report.

— & HOLT, S. J., in press: "On the dynamics of exploited fish populations". Min. Agric. Fish., Fish. Invest., Ser. 2, **19**.

BJERKAN, P., 1917: "Age, maturity and quality of North Sea herrings during the years 1910—13". Rep. Norw. Fish. Mar. Invest., **3**. 1.

BOEREMA, L. K., 1950: "The Dutch fishery for demersal seafish in 1949". Cons. Internat. Explor. Mer, Ann. Biol., **6**, pp. 126—130.

BOHL, H., 1954: "Die Verbreitung der Schollenbrut in der südlichen Nordsee im März 1953 in ihrer Abhängigkeit von der hydrographischen Situation". Kurze Mitt. Inst. Fischereibiol. Univ. Hamburg, 4, pp. 18—37.

BORLEY, J. O. & RUSSELL, E. S., 1922: "Report on herring trawling". Min. Agric. Fish., Fish. Invest., Ser. 2, **4**, 4.

BOWMAN, A., 1932: "The effect on the stock of the capture of undersized fish". Cons. Internat. Explor. Mer, Rapp. et Proc.-Verb., **80**, III.

— 1932: "A comparison of the Vigneron-Dahl trawling gear with the ordinary otter trawl in the haddock fishery". Ibid., **80**, III, App. B.

v. BRANDT, A., 1953: "Untersuchungen über die Fängigkeit von Stellnetzen unter Berücksichtigung der Netzfarbe". Arch. Fischereiwiss., **4**, 1, pp. 5—18.

BUCHANAN-WOLLASTON, H. J., 1927: "On the selective action of a trawl net, with some remarks on the selective action of drift nets". Journ. du Cons., **2**, 3, pp. 343—55.

CAMERON, J. M., 1951: "The use of components of variance in preparing schedules for sampling of baled wool". Biometrics, **7**, pp. 83—96.

CHAPMAN, D. G., 1948: "A mathematical study of confidence limits of salmon populations calculated from sample tag ratios". Bull. Internat. Pacif. Salmon Fish. Comm., **2**, 2, pp. 67—85.

CLARK, J. R., 1952: "Experiments on the escape of undersized haddock through otter trawls". Comm. Fish. Rev., **14**, 9, pp. 1—7.

CLOPPER, C. J. & PEARSON, E. S., 1934: "The use of confidence or fiducial limits illustrated in the case of the binomial". Biometrika, **26**, pp. 404—13.

COCHRAN, W. G., 1939: "The use of analysis of variance in enumeration by sampling". Journ. Amer. Statist. Assoc., **34**, pp. 492—510.

— 1942: "Sampling theory when the sampling units are of unequal sizes". Ibid., **37**, pp. 199—212.

— 1953: "Sampling techniques". J. Wiley & Sons, Inc., New York.

CUSHING, D. H., 1953: "Studies on plankton populations". Journ. du Cons., **19**, 1, pp. 3—22.

DAVIS, F. M., 1934: "Mesh experiments with trawls, 1928—33". Min. Agric. Fish., Fish. Invest., Ser. 2, **14**, 1.

DELSMAN, H. C., 1914: "Über das Wachstum von Nordseehering und Zuiderzeehering nach Untersuchungen an den Schuppen". Rapp. en Verhandl. Rijksinst. Visscherijonderz., **1**, pp. 133—200.

DELURY, D. B., 1951· "On the planning of experiments for the estimation of fish populations". Journ. Fish. Res. Brd. Canada, **8**, 4, pp. 281—307.

DEMING, W. E., 1950: "Some theory of sampling". J. Wiley & Sons, Inc., New York.

EDSER, T., 1908: "Note on the number of plaice at each length, in certain samples from the southern part of the North Sea, 1906." Journ. Roy. Stat. Soc., **71**, pp. 686—90.

EISENHART, C., 1947: "The assumptions underlying the analysis of variance". Biometrics, **3**, pp. 1—21.

FINNEY, D. J., 1941: "On the distribution of a variate whose logarithm is normally distributed". Journ. Roy. Stat. Soc., Suppl., 7 pp. 155—61.

— 1946: "Field sampling for the estimation of wireworm populations". Biometrics, **2**, pp. 1—7.

FISHER, R. A., 1925: "Statistical methods for research workers". Oliver & Boyd, Edinburgh.

— & YATES, F., 1938: "Statistical tables for biological, agricultural and medical research". Oliver & Boyd, Edinburgh.

FRIÐRIKSSON, Á., 1934: "On the calculation of age-distribution within a stock of cod by means of relatively few age-determinations as a key to measurements on

a large scale". Cons. Internat. Explor. Mer, Rapp. et Proc.-Verb., **86**, 6.

FRY, F. E. J., 1949: "Statistics of a lake trout fishery". Biometrics, **5**, pp. 27—67.

FULTON, T. W., 1920: "Report on the marking experiments on plaice, made by the S/S 'Goldseeker', in the years 1910—1913". Sci. Invest. Fish. Scotl., 1919, 1.

— 1922: "Report on herring trawling investigations". Ibid., 1921, 2.

GILIS, CH., 1953: "Full-herring concentrations exploited by the Belgian herring trawlers in 1952". Cons. Internat. Explor. Mer, Ann. Biol., **9**, pp. 196—200.

GRAHAM, M., 1934: "Report on the North Sea cod". Min. Agric. Fish., Fish. Invest., Ser. 2, **13**, 4.

— 1935: "Modern theory of exploiting a fishery, and application to North Sea trawling". Journ. du Cons., **10**, 3, pp. 264—74.

— 1952: "Overfishing and optimum fishing". Cons. Internat. Explor. Mer, Rapp. et Proc.-Verb., **132**, pp. 72—8.

— 1954: "Trials of mesh selection in trawls and seines". Journ. du Cons., **20**, 1, pp. 62—71.

GRAY, P. G. & CORLETT, T., 1950: "Sampling for the social survey". Journ. Roy. Stat. Soc., A, **113**, pp. 150—206.

GULLAND, J. A., 1952: "Plaice: British landings, 1950 and 1951". Cons. Internat. Explor. Mer, Ann. Biol., **8**, pp. 109—11.

— 1955: "Estimation of growth and mortality in commercial fish populations". Min. Agric. Fish., Fish. Invest., Ser. 2, **18**, 9.

HANSEN, M. H. & HURWITZ, W. N., 1943: "On the theory of sampling from finite populations". Ann. Math. Statist., **14**, pp. 333—62.

— — 1949: "On the determination of the optimum probabilities in sampling". Ibid., **20**, pp. 426—32.

HICKLING, C. F., 1937: "The English plaice marking experiments, 1929—32". Min. Agric. Fish., Fish. Invest., Ser. 2, **16**, 1.

— 1946: "The recovery of a deep sea fishery". Ibid., **17**, 1.

HILE, R., 1936: "Age and growth of the cisco *Leucichthys artedi* (LESUEUR) in the lakes of the north-eastern highlands, Wisconsin". Bull. U.S. Bur. Fish. **48**, 19, pp. 211—318.

HODGSON, W. C., 1927: "Preliminary note on experiments concerning the selective action of drift nets". Journ. du Cons., **2**, 3, pp. 356—60.

— 1933: "Further experiments on the selective action of commercial drift nets". Ibid., **8**, 3, pp. 344—54.

— 1939: "An improved method of sampling herring shoals." Cons. Internat. Explor. Mer, Rapp. et Proc.-Verb., **110**, pp. 31—80.

HOEL, P. G., 1943: "The accuracy of sampling methods in ecology". Ann. Math. Statist., **14**, pp. 289—300.

HOLT, S. J., 1949: "The fishing intensity on the plaice stock of the southern North Sea". Cons. Internat. Explor. Mer, Ann. Biol., **4**, p. 111.

JENSEN, AA. J. C., 1939: "On the laws of decrease in fish stocks". Cons. Internat. Explor. Mer, Rapp. et Proc.-Verb., **110**, pp. 86—96.

JESSEN, R. J., *et al.*, 1947: "On a population sample for Greece". Journ. Amer. Statist. Assoc., **42**, pp. 357—84.

JONES, R., 1951: "Haddock". Cons. Internat. Explor. Mer, Ann. Biol., **7**, pp. 28—31.

— & MAIN, W., 1951: Ibid., **7**, pp. 77—80.

— — 1952: Ibid., **8**, pp. 36—9 and pp. 105—6.

— — 1953: Ibid., **9**, pp. 35—8 and pp. 127—9.

— — 1954: Ibid., **10**, pp. 32—5 and pp. 108—9.

JURKOVICH, J., 1954: "Selectivity of cod-end mesh sizes in otter trawling". Wash. Dept. Fish., Fish. Res. Pap., **1**, 2, pp. 19—24.

KENNEDY, W. A., 1951: "The relationship of fishing effort by gill nets to the interval between lifts". Journ. Fish. Res. Brd. Canada, **8**, 4, pp. 264—74.

KURITA, S., 1948: "A theoretical consideration on the method for estimating survival rate of a fish stock by using the age difference between the oldest and the average". Contrib. Cent. Fish. Stat. Japan, 37.

KYLE, H. M., 1903: "Fishing nets, with special reference to the otter trawl". Journ. Mar. Biol. Assoc. U.K., **6**, pp. 562—86.

LINDLEY, D. V. & MILLER, J. C. P., 1953: "Cambridge elementary statistical tables". Cambridge University Press.

LOTKA, A. J., 1925: "Elements of physical biology". 460 pp. Williams and Williams Co., Baltimore.

LUCAS, C. E., 1936: "On the diurnal variation of size-groups of trawl-caught herring". Journ. du Cons., **11**, 1, pp. 53—9.

MAHALANOBIS, P. C., 1944: "On large scale sample surveys". Roy. Soc. Phil. Trans., B, **231**, pp. 329—451.

MARGETTS, A. R., 1949 a: "Experimental comparison of fishing capacities of different trawlers and trawls". Cons. Internat. Explor. Mer, Rapp. et Proc.-Verb., **125**, pp. 72—81.

— 1949 b: "Experimental comparison of fishing capacities of Danish-seiners and trawlers". Ibid., **125**, pp. 82—90.

MARR, J. C., 1950: "Apparent abundance of the pilchard (*Sardinops caerulea*) off Oregon and Washington, 1935—43, as measured by the catch per boat". U.S. Dept. Int., Fish & Wildl. Serv., Fish. Bull., **51**, 52, pp. 385—94.

MCCARTHY, P. J., 1951: "Sampling, elementary principles". Bull. New York State School Indust. Lab. Relat., 15.

MOORE, H. L., 1951: "Estimation of age and growth of yellowfin tuna (*Neothunnus macropterus*) in Hawaiian waters by size frequencies". U.S. Dept. Int., Fish & Wildl. Serv., Fish. Bull., **52**, 65, pp. 133—49.

NEYMANN, J., 1934: "On the two different aspects of the representative method: the method of stratified sampling and the method of purposive selection". Journ. Roy. Stat. Soc., **97**, pp. 558—606.

PARRISH, B. B., 1949: "Fishing capacities of gears used by English and Scottish research vessels". Cons. Internat. Explor. Mer, Rapp. et Proc.-Verb., **125**, pp. 91—6.

— 1951: "Fishing capacities of Lowestoft and Aberdeen trawls when used on flatfish grounds". Journ. du Cons., **17**, 2, pp. 156—69.

— & MAIN, W., 1950: "Haddock. Scottish investigations". Cons. Internat. Explor. Mer, Ann. Biol., **6**, pp. 101—6.

— & POPE, J. A., 1951: "Further results on the effect of using small-mesh covers: effects on the catches of the escape sizes of fish". I.C.E.S. Meeting 1951.

— & JONES, R., 1953: "Haddock bionomics. I. The state of the haddock stocks in the North Sea 1946—1950 and at Faroe 1914—50". Scot. Home Dept., Mar. Res., 1952, 4.

PETRIDES, G. A., 1949: "View-points on the analysis of open season sex and age ratios". Trans. 14th N. Amer. Wildl. Conf., pp. 391—410.

POPE, J. A., 1952: "The effect of sweeps and small mesh cover on catch". Unpubl. report.

— 1953: "Cod-end and cover experiment". Unpubl. report.

PRUTER, A. T. & VAN CLEVE, R., 1954: "A preliminary study of the population of English sole, *Parophrys vetulus*, in Holmes Harbour, Washington". Wash. Dept. Fish., Fish. Res. Pap., **1**, 2, pp. 3—18.

RICKER, W. E., 1944: "Further notes on fishing mortality and effort". Copeia, 1944, 1, pp. 23—44.
— 1948: "Methods of estimating vital statistics of fish populations". Indiana Univ. Publ., Sci. Ser., 15.
— 1949: "Mortality rates in some little exploited populations of fresh-water fishes". Trans. Amer. Fish. Soc., **77**, pp. 114—28.
ROLLEFSEN, G., 1935: "The spawning zone in cod otoliths and prognosis of stock". Fiskeridirekt. Skr., **4**, 11, pp. 3—10.
— 1953: "The selectivity of different fishing gear used in Lofoten". Journ. du Cons., **19**, 2, pp. 191—4.
ROUNSEFELL, G. A., 1948: "Development of fishery statistics in the North Atlantic". U.S. Dept. Int., Fish and Wildl. Serv., Spec. Sci. Rep., 47.
— 1949: "Methods of estimating total runs and escapements of salmon". Biometrics, **5**, 2, pp. 115—26.
RUSSELL, E. S., 1931: "Some theoretical considerations on the 'overfishing problem'". Journ. du Cons., **6**, 1, pp. 3—20.
SCHAEFER, M. B., 1951: "Estimation of size of animal populations by marking experiments". U.S. Dept. Int., Fish and Wildl. Serv., Fish. Bull., **52**, 69, pp. 189—203.
— 1953: "Report on the investigations of the Inter-American Tropical Tuna Commission during the year 1952". Inter-Amer. Tropic. Tuna Comm., Ann. Rep. 1952, App. A, p. 14.
— 1954: "Some aspects of the dynamics of populations important to the management of the commercial marine fisheries". Ibid., Bull., **1**, 2, pp. 27—56.
SCHUMACHER, F. X. & CHAPMAN, R. A., 1942: "Sampling methods in forestry and range management". Duke Univ., Durham, North Carolina.
SHETTER, D. S., 1952: "The mortality and growth of marked and unmarked lake trout fingerlings in the presence of predators". Trans. Amer. Fish. Soc., **81**, pp. 17—34.
SILLIMAN, R. P., 1943: "Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). 5. A method of computing mortalities and replacements". U.S. Dept. Int., Fish and Wildl. Serv., Spec. Sci. Rep., 24.
— 1945: "Determination of mortality rates from length frequencies of the pilchard or sardine (*Sardinops caerulea*)". Copeia, 1944, 4, pp. 191—6.
— & CLARK, F. N., 1945: "Catch per-unit-of-effort in California waters of the sardine (*Sardinops caerulea*) 1932—1942". Calif. Div. Fish and Game, Fish Bull., 62.
SIMPSON, A. C., 1951: "The fecundity of the plaice". Min. Agric. Fish., Fish. Invest., Ser. 2, **17**, 5.
— 1952: "Studying the eggs and young of fish". World Fishing, **1**, 8, pp. 283—6.
SMITH, H. F., 1947: "Standard errors of means in sampling surveys with two-stage sampling". Journ. Roy. Statist. Soc., **110**, pp. 257—9.
TANAKA, S., 1953: "Precision of age-composition of fish estimated by double sampling method using the length for stratification". Bull. Japan. Soc. Sci. Fish., **19**, 5, pp. 657—70.
TAUTI, M., 1947: "An estimation of the apparent survival rate by finding of the maximum and the mean values of the age, weight and length". Bull. Japan. Soc. Sci. Fish., **13**, 3, pp. 91—4.
TAYLOR, C. C., 1953: "Nature and variability in trawl catches". U.S. Dept. Int., Fish and Wildl. Serv., Fish. Bull., **54**, 83, pp. 145—66.
THIONET, P., 1946: "Méthodes statistiques modernes des administrations fédérales aux Etats-Unis". Herman & Cie., Paris.
THOMPSON, W. F., 1950: "The effect of fishing on the stocks of halibut in the Pacific". Publ. Fish. Res. Inst., Univ. Washington, Seattle.
— & HERRINGTON, W. C., 1930: "Life history of the Pacific halibut. 1. Marking experiments". Rep. Internat. Fish. Comm., 2.
— , DUNLOP, H. A. & BELL, F. H., 1931: "Biological statistics of the Pacific halibut fishery. 1. Changes in yield of a standardized unit of gear". Ibid., 6.
— & BELL, F. H., 1934: "Biological statistics of the Pacific halibut fishery. 2. Effect of changes in the intensity upon total yield per unit of gear". Ibid., 8.
THURSBY-PELHAM, D. E., 1939: "The effect of fishing on the stocks of plaice in the North Sea". Cons. Internat. Explor. Mer, Rapp. et Proc.-Verb., **110**, pp. 40—63.
TUKEY, J. W., 1950: "Some sampling simplified". Journ. Amer. Statist. Assoc., **45**, pp. 501—19.
VOLTERRA, V., 1928: "Variations and fluctuations of the number of individuals in animal species living together". Journ. du Cons., **3**, 1, pp. 3—51.
WEATHERBURN, C. E., 1949: "A first course in mathematical statistics". p. 54, University Press, Cambridge.
WIDRIG, T. M., 1954: "Definitions and derivations of various common measures of mortality rates relevant to population dynamics of fishes". Copeia, 1954, 1, pp. 29—32.
WINSOR, C. P. & CLARKE, G. L., 1940: "A statistical study of variation in the catch of plankton nets". Journ. Mar. Res., **3**, pp. 1—34.
YAMAMOTO, T., 1953: "Sampling survey of fisheries catch statistics in Japan". Stat. & Surv. Div., Jap. Min. Agric. & Forestry.
YATES, F., 1935: "Some examples of biased sampling". Ann. Eugen., **6**, pp. 202—13.
— 1949: "Sampling methods for censuses and surveys". C. Griffin & Co. Ltd., London.
— & ZACOPANAY, I., 1935: "The estimation of the efficiency of sampling, with special reference to sampling for yield in cereal experiments". Journ. Agric. Sci., **25**, pp. 545—77.
— & FINNEY, D. J., 1942: "Statistical problems in field sampling for wireworms". Ann. Appl. Biol., **29**, pp. 156—67.